

Anatomical Characteristics and Natural Durability of Three Korean Diffuse-porous Hardwood Species

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Natural durability is an important wood property that influences utilization potential. This study investigated the anatomical characteristics and natural durability of three Korean diffuse-porous hardwood species, namely *Betula platyphylla*, *Liriodendron tulipifera*, and *Quercus salicina*, to assess whether measurable anatomical traits could serve as indicators of durability. Traits were measured using microscopic image analysis, and natural durability was evaluated using fungal decay and termite resistance tests. Associations between anatomical traits and durability were explored using multiple factor analysis (MFA). Among the species examined, *L. tulipifera* exhibited the lowest fungal weight loss and highest termite resistance, whereas *B. platyphylla* showed the greatest susceptibility to fungal decay and termite attack. The MFA suggested exploratory associations, based on species-level data from three species, between fungal decay resistance and vessel-related anatomical traits, whereas termite resistance showed limited correspondence with the anatomical variables examined. These results suggest an exploratory relationship between vessel dimensions and variation in fungal decay susceptibility among the three species; anatomical traits corresponded only weakly with overall natural durability. The findings may support future wood informatics research and facilitate the development of data-driven models that integrate anatomical, physical, and chemical datasets to predict wood properties.

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INTRODUCTION

Diffuse-porous wood species are characterized by vessels that are relatively uniform in size throughout the annual growth ring. Such wood species are predominantly found in the tropical and temperate regions of America, Africa, and Asia (Wardle 1991). Because of their homogeneous vessel distribution, diffuse-porous wood species usually exhibit a relatively uniform appearance and more homogeneous mechanical features than ring-porous species (Zhan *et al.* 2015; Esteban *et al.* 2024). Such characteristics facilitate the prediction of mechanical properties and contribute to relatively consistent stress transfer within wood products (de Borst and Bader 2014; Zhan *et al.* 2015).

These features are advantageous for the manufacture of engineered wood products, such as glued laminated timber and laminated veneer lumber, where uniform adhesive performance and strength distribution are beneficial (Yelle and Stirgus 2016; Morin-Bernard *et al.* 2020). Furthermore, the relatively uniform anatomical structure of diffuse-porous wood species has recently attracted attention in the development of high-strength densified wood materials (Mania *et al.* 2024).

In Korea, three diffuse-porous hardwood species, namely *Betula platyphylla*, *Liriodendron tulipifera*, and *Quercus salicina*, are recommended for afforestation (Korea Forest Service 2025). Previous studies have examined various properties of *B. platyphylla* and *L. tulipifera*, including wood anatomy, mechanical performance, durability, and acoustic behavior (Kang *et al.* 2011; Zhan *et al.* 2015; Erdene-Ochir *et al.* 2021; Esteban *et al.* 2024; Jung *et al.* 2025). However, quantitative information linking the anatomical characteristics with natural durability among these diffuse-porous hardwood species remains limited, particularly for *Q. salicina*.

The natural durability of wood varies considerably among species and is primarily influenced by the type and composition of its extractives present in the wood (Rodrigues *et al.* 2011; Amusant *et al.* 2014). Certain extractives possess antimicrobial and insecticidal properties that improve resistance to wood-decaying fungi and termites. Previous studies have demonstrated that the removal of extractives substantially decreases resistance to biological deterioration (Scheffer and Cowling 1966; Smith *et al.* 1989; Kirker *et al.* 2013). Furthermore, durability is determined by the quantity, chemical profile, and spatial allocation of extractives, leading to considerable variation even within the same species (Scheffer and Cowling 1966; Kirker *et al.* 2013).

In addition to chemical composition, anatomical characteristics, such as vessel structure, cell wall thickness (CWT), tissue arrangement, and wood density, have recently been recognized as important factors influencing wood durability (Dadzie and Amoah 2015; De Ligne *et al.* 2021). Previous studies have suggested that parenchyma content and the vessel-to-fiber ratio are associated with resistance to brown-rot fungi, whereas other anatomical traits are closely related to wood density and mechanical performance (De Ligne *et al.* 2021). Based on these findings, we expected differences in vessel and fiber characteristics, particularly vessel dimensions and cell wall thickness, to be associated with variation in natural durability.

Traditionally, the anatomical characteristics of wood have been extensively used for species identification and taxonomic studies. Recent advances in digital microscopy and image analysis have improved the accuracy and reproducibility of quantitative anatomical assessments (von Arx *et al.* 2016; Frigo *et al.* 2024). These developments have increased the availability of anatomical datasets that can be integrated with data-driven approaches to predict wood properties and performance (He *et al.* 2024; Keret *et al.* 2024). Consequently, understanding how the anatomical characteristics of wood relate to natural durability has become increasingly important in scientific research and functional applications.

Therefore, the anatomical characteristics and natural durability of three diffuse-porous hardwood species commonly used in Korean forestry were investigated. Specifically, this study examined whether variation in quantitative anatomical traits was associated with fungal decay and termite resistance, and we assessed the potential of these traits as practical indicators of natural durability.

EXPERIMENTAL

Wood Materials

Betula platyphylla Sukaczew, *Liriodendron tulipifera* Linnaeus, and *Quercus salicina* Blume were used in this study; the sampling sites were Hongcheon-gun in Gangwon-do, Gangjin-gun in Jeollanam-do, and Sacheon-si in Gyeongsangnam-do, respectively (Table 1). For each species, a single tree was sampled at the corresponding site. A wood disk was obtained from each stem at breast height (approximately 1.3 m), and its cross-sectional surface was polished for subsequent analyses. The collected disks contained 35, 28, and 16 growth rings for *B. platyphylla*, *L. tulipifera*, and *Q. salicina*, respectively. The cross-sections and the edge- and flat-grain surfaces of three wood species are shown in Fig. 1.

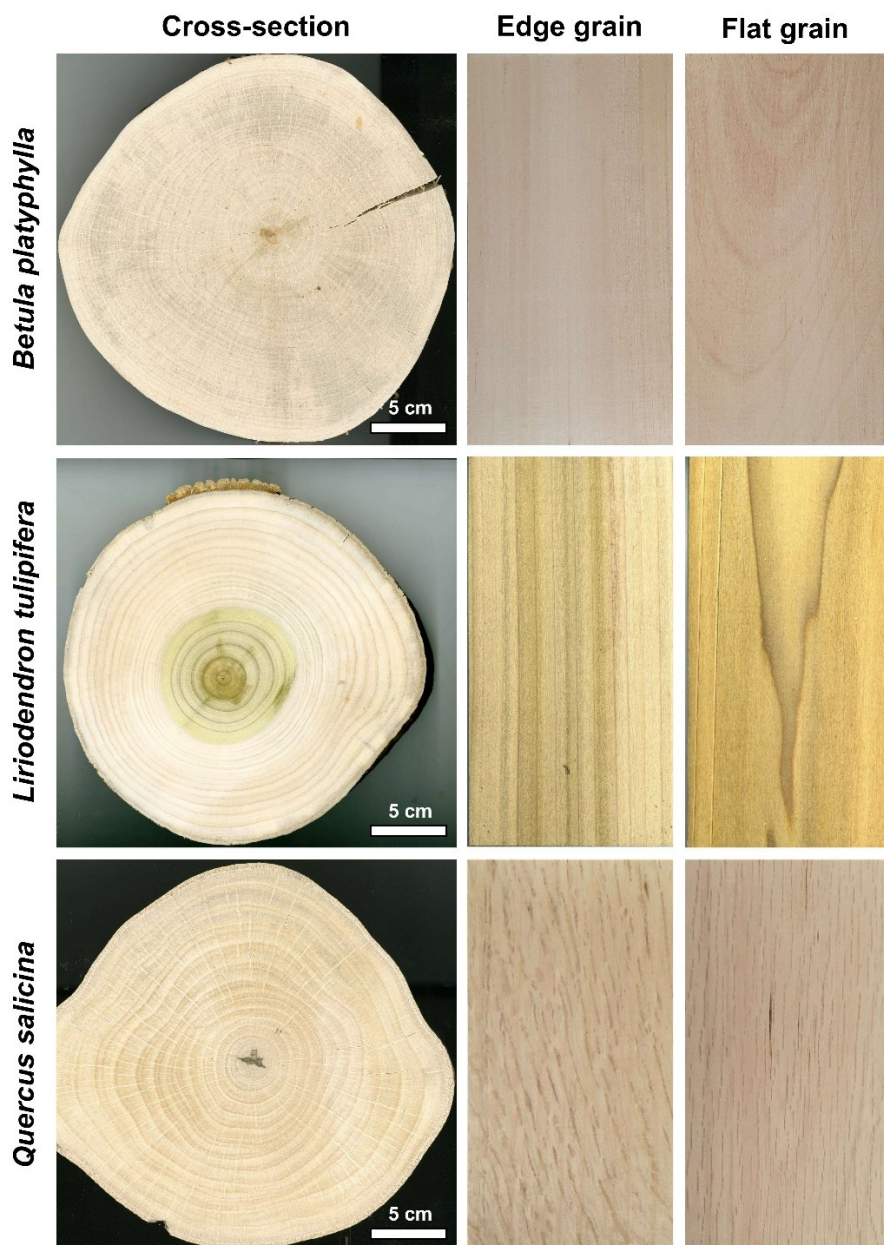


Fig. 1. Cross-section, edge-grain, and flat-grain surfaces of three hardwood species

Wood blocks for anatomical trait analysis were taken from the mature-wood zone of each disk. The exact number of blocks prepared per species and their precise radial positions within the mature-wood zone (near-pith, intermediate, or near-bark) were not documented. Because the *Q. salicina* disk contained no mature wood (defined as ≥ 20 growth rings from the pith), blocks for this species were obtained from juvenile wood instead. Specimens for the fungal decay test were taken from sapwood, whereas those for the termite test were taken from heartwood. These specimens were cut from the same breast-height disk, but their exact radial positions were not recorded.

Table 1. Site Characteristics for the Three Sampling Locations

Species	Region	Mean annual temperature (°C)	Mean annual relative humidity (%)	Mean annual precipitation (mm)
<i>Betula platyphylla</i>	Hongcheon-gun, Gangwon-do	11.5	68	1280
<i>Liriodendron tulipifera</i>	Gangjin-gun, Jeollanam-do	14.2	73	1360
<i>Quercus salicina</i>	Sacheon-si, Gyeongsangnam-do	13.7	68	1540
Climate data represent the mean values for the period 2006 to 2025 and were obtained from the Korea Meteorological Administration (https://data.kma.go.kr). As climate data for Sacheon-si were unavailable, data from the nearest available location, Jinju-si, were used as representative climate data for the Sacheon-si sampling site.				

Annual Ring Width and Anatomical Trait Analysis

The cross-section of the wood disc was divided into four sections with two perpendicular lines and scanned using an Epson Expression 10000XL scanner (EU-88, Seiko Epson Corp., Suwa, Japan) to obtain an image. The annual ring width (ARW) was measured from the pith to the bark using DeltaPix v5.3.11.

Anatomical traits were analyzed using the wood blocks (10 mm × 10 mm × 10 mm in the longitudinal (L), tangential (T), and radial (R) directions) prepared from the mature-wood zone of each disk (juvenile wood for *Q. salicina*). Following Park *et al.* (2024a, 2024b), the blocks were sectioned longitudinally with a razor blade. Subsequently, the sections were macerated in Franklin's solution (a 1:1 (v/v) mixture of 30% H₂O₂ and 95% CH₃COOH) and heated at 80 °C on a heating mantle for 48 h. The macerated vessel and fiber elements were stained with methylene blue to improve cellular contrast, and their lengths were measured using DeltaPix software v5.3.11. For measurements of cell wall thickness (CWT) and widths in the radial (D_{rad}) and tangential (D_{tan}) directions, thin transverse sections (10 to 20 µm thick) were prepared using a sliding microtome, stained with 1% safranin, dehydrated through a graded ethanol series, and permanently mounted in Canada balsam for microscopic examination. The traits of vessels and fibers were measured on the stained sections with the same software. For each of the eight anatomical traits, 30 measurements were obtained from the single tree sampled per species, resulting in 240 anatomical measurements per species. These measurements therefore reflect within-tree variation rather than independent tree-level biological replicates.

Durability Test Against Wood-decaying Fungi

The durability test against wood-decaying fungi was conducted according to the guidelines outlined in the Assessment Manual for Domestic Wood Characteristics (Park *et al.* 2024c). The guidelines were based on KS F 2213 (2018). The fungus was pre-cultured on potato dextrose agar at 26 ± 2 °C for 2 weeks in the dark. Five 10-mm-diameter plugs were then excised from the actively growing margins of the pre-cultured mycelium and inoculated into 100 mL of liquid culture medium adjusted to pH 5.5 to 6.0. The medium consisted of glucose (40 g/L), malt extract (15 g/L), and peptone (3 g/L), supplemented with 0.3 g of 100-mesh pine sapwood powder. All culture media were sterilized prior to use. The inoculated cultures were incubated on a rotary shaker at 26 ± 2 °C for 1 week in the dark and subsequently used for the test.

Twelve sapwood specimens each of *B. platyphylla* and *Q. salicina* and nine of *L. tulipifera* ($9 \times 25 \times 25$ mm, $L \times T \times R$) were used for the fungal decay test. Three specimens were placed in each culture vessel, resulting in four culture vessels each for *B. platyphylla* and *Q. salicina* and three for *L. tulipifera*. In addition, 30 sapwood specimens of *Carpinus laxiflora* were prepared as controls to monitor the test endpoint.

For the test, cylindrical glass vessels with a bottom surface area of approximately 50 to 100 cm² and a volume of 500 to 800 mL were used. Each culture vessel was filled with 250 g of sea sand and 80 mL of the same liquid culture medium used for fungal cultivation, and the vessels were sterilized prior to use. The fungus grown in shake culture was thoroughly suspended, and 3 mL of the suspension was inoculated into each culture vessel. The inoculated vessels were incubated at 26 ± 2 °C and 70% relative humidity in the dark until the mycelium completely covered the sand surface. Subsequently, three gas-sterilized wood specimens were placed in each culture vessel, and their fungal decay resistance was evaluated under the same incubation conditions.

After 8 weeks of incubation, three control specimens were randomly removed from the culture vessels, and their weight loss (WL) was measured to determine whether the test endpoint had been reached. Thereafter, three further control specimens were randomly removed at 1-week intervals, and the test was terminated when their mean WL reached 50%. To determine WL, the specimens were dried at 60 ± 2 °C for 48 h and then cooled in a desiccator for 30 min before being weighed to the nearest 0.01 g. The same procedure was applied before and after the decay test, and WL (%) was calculated according to Eq. (1).

$$WL (\%) = (w_1 - w_2) / w_1 \times 100 \quad (1)$$

where w_1 and w_2 are the oven-dried weights (g) before and after the decay test, respectively.

Durability Test Against Termites

The durability test against termites was conducted in accordance with the guidelines outlined in the Assessment Manual for Domestic Wood Characteristics (Park *et al.* 2024c). The guidelines were based on AWP A E1-17 (2017). Subterranean termites (*Reticulitermes speratus*), which are distributed throughout South Korea, were used in this study. Five heartwood specimens each were prepared for *B. platyphylla* and *L. tulipifera* and seven for *Q. salicina*, all measuring $6.4 \times 25.4 \times 50.8$ mm ($L \times T \times R$).

Prior to the test, the specimens were sterilized with ethylene oxide gas for at least 5 h at room temperature and then conditioned at 20 ± 2 °C and $65 \pm 3\%$ relative humidity until exposure to termites. After the specimens reached a constant weight, they were weighed to the nearest 0.01 g. Each specimen was then cut into two pieces measuring 6.4

$\times 25.4 \times 25.4$ mm (L $\times$ T $\times$ R): one for the termite resistance test and the other for moisture content (MC) determination. The pieces used for MC determination were oven-dried at 103 ± 2 °C for 24 h and weighed to calculate the MC and oven-dry mass of the wood.

Throughout the termite resistance test, the sea sand in the culture vessels was maintained at a constant moisture level corresponding to 7% below its water saturation level. The water saturation level of the sea sand was determined by oven-drying 100 g of the sand at 103 °C for 24 h and subsequently adding distilled water until water became visible above the sand surface. The water saturation level was calculated according to Eq. (2),

$$\text{Water saturation level (\%)} = (W_{\text{water}} / W_{\text{sand}}) \times 100 \quad (2)$$

where W_{water} is the mass of distilled water added until water became visible above the sand surface (g), and W_{sand} is the oven-dry mass of the sea sand (g).

For the termite resistance test, 150 g of oven-dried sea sand was placed in each clean culture vessel, followed by the calculated amount of distilled water. The vessels were maintained at room temperature for 2 h to allow the water to distribute throughout the sand. One test specimen was then placed in each vessel with its cross-sectional surface on the sand and one edge against the side of the vessel. Additional culture vessels without wood specimens were prepared to monitor termite activity.

A total of 400 termites, consisting of 396 workers and four soldiers, were introduced into each culture vessel. The termites were placed on the side of the vessel opposite the wood specimen. Once the termites were introduced, the total mass of each culture vessel was recorded and used as a reference for replenishing water when necessary.

The culture vessels were maintained at 26 ± 2 °C and $\geq 70\%$ relative humidity for 4 weeks. Termite activity was monitored throughout the exposure period, and water was replenished as needed to maintain adequate moisture. After 1 week of exposure, termite viability was confirmed in the monitoring vessels.

After 4 weeks of exposure, termite damage was visually evaluated according to AWP A E1-17 (AWPA 2017) using the following rating scale: 10, sound; 9.5, trace attack with surface nibbles permitted; 9, light attack with up to 3% of the cross-sectional area affected; 8, moderate attack with 3 to 10% affected; 7, moderate to severe attack with penetration and 10 to 30% affected; 6, severe attack with 30 to 50% affected; 4, very severe attack with 50 to 75% affected; and 0, failure. After visual assessment, the specimens were oven-dried at 103 ± 2 °C for 24 h, cooled in a desiccator for 30 min, and weighed to the nearest 0.01 g. WL (%) was then calculated according to Eq. (1) with w_1 taken as the oven-dry mass estimated from the paired MC piece. Finally, the surviving termites in each culture vessel were counted, and termite mortality was calculated according to Eq. 3,

$$\text{Termite mortality (\%)} = [(N_{\text{initial}} - N_{\text{surviving}}) / N_{\text{initial}}] \times 100 \quad (3)$$

where N_{initial} is the initial number of termites introduced into each vessel and $N_{\text{surviving}}$ is the number of surviving termites after the exposure period.

Statistical Analysis

All statistical analyses were conducted using R v4.5.1 (R Core Team 2025). Differences in anatomical traits and durability among the three wood species were tested at a significance level of $\alpha = 0.05$ (95% confidence level). For each anatomical trait, 30

measurements were obtained from the sampled tree of each species and used in the statistical analyses. Prior to testing, the normality and homogeneity of variance of ARW, the anatomical traits, and the durability data were assessed using the Shapiro–Wilk and Levene’s tests, respectively.

Variables satisfying both assumptions were analyzed using one-way analysis of variance (ANOVA) followed by Tukey’s honestly significant difference (HSD) test. Those that violated either assumption were analyzed with the non-parametric Kruskal–Wallis test followed by Dunn’s post-hoc test with Benjamini–Hochberg correction for pairwise comparisons.

Because only one tree was sampled per species, the 30 measurements represent within-tree anatomical variation rather than independent tree-level biological replicates. Therefore, species, individual-tree, and site effects could not be separated, and the statistical comparisons were interpreted as exploratory.

Multiple factor analysis (MFA) was conducted with the FactoMineR package in R to investigate the multivariate associations among four predefined trait blocks: anatomical traits, ARW, WL by fungal decay, and WL by termite attack. Prior to MFA, measurements were averaged at the species level, and all variables were standardized to unit variance. The MFA was used to evaluate the relative contribution of each trait block to the major dimensions of multivariate variation and visualize associations among species and trait variables in a shared ordination space.

RESULTS AND DISCUSSION

Qualitative and Quantitative Anatomical Features

The three hardwood species exhibited diffuse-porous wood structures with distinct growth rings (Figs. 2 to 4). *B. platyphylla* had vessels that were mostly solitary or occasionally arranged in radial multiples (Fig. 2A and D). In the radial section, the rays were composed entirely of procumbent cells, and the perforation plates were scalariform (Fig. 2B, E, and F). Vessel-ray pits were rounded to angular, with much reduced to apparently simple borders (Fig. 2F).

In the tangential section, the inter-vessel pits were arranged in opposite to alternate patterns (Fig. 2C and G). *L. tulipifera* contained numerous vessels that were mostly arranged in radial multiples, although solitary vessels were also observed (Fig. 3A and D). In the radial section, the homocellular rays consisted of procumbent cells, whereas the heterocellular rays consisted of procumbent and square-marginal cells (Fig. 3B, E, F, and G). The perforation plates were either simple or scalariform (Fig. 3B and G).

Vessel-ray pits were rounded to angular, with much reduced to apparently simple borders (Fig. 3G). In the tangential section, inter-vessel pits were arranged in opposite patterns (Fig. 3C and H). *Q. salicina* contained mostly solitary vessels, with some arranged in a radial pattern (Fig. 4A and D). In the radial section, the rays were composed of procumbent cells, and the perforation plates were simple (Fig. 4B and E). Vessel-ray pits were rounded to angular and horizontally elongated, ranging from scalariform to gash-like, or vertically elongated to palisade-like, with much reduced to apparently simple borders (Fig. 4F). In the tangential section, inter-vessel pits were arranged in alternate patterns (Fig. 4C and G).

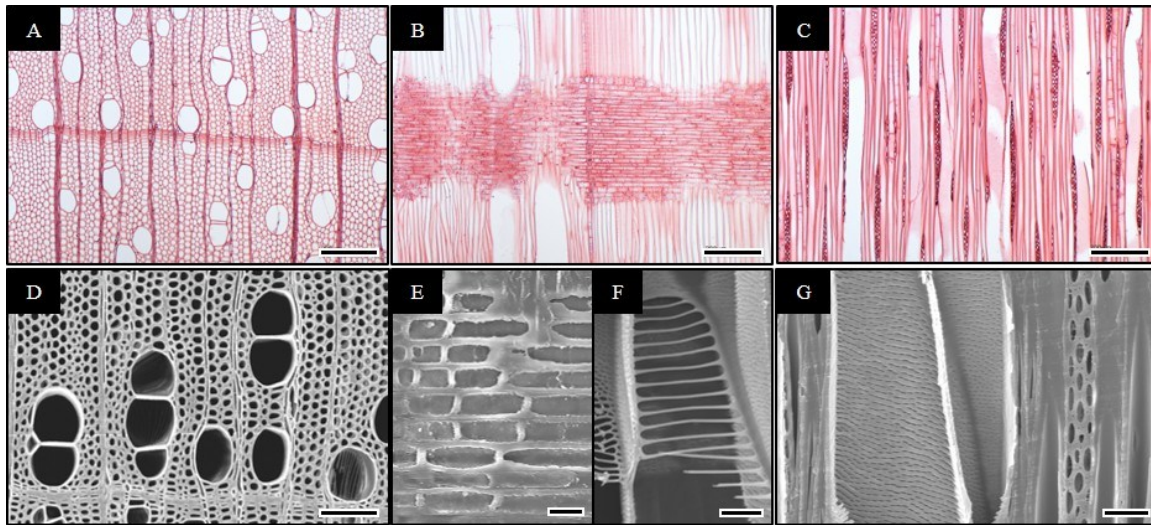


Fig. 2. Anatomical structures of *Betula platyphylla*: (A to C) Light micrographs; (D to G) scanning electron micrographs; Cross-sections (A, D) show vessel elements arranged in radial alignment; Radial surfaces (B, E, and F) show rays composed of procumbent cells (E), scalariform perforation plates, and vessel-ray pits rounded to angular, with much reduced to apparently simple borders (F); Tangential surfaces (C, G) show vessel elements with opposite and alternate inter-vessel pits (G); Scale bars: (A to C) = 200 μm ; (D) = 100 μm ; (E to G) = 20 μm

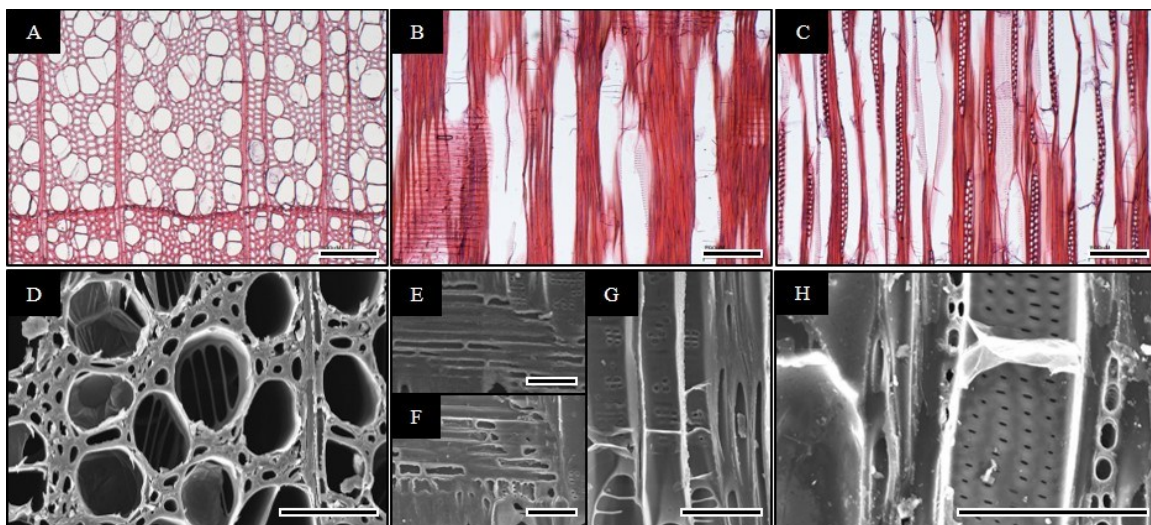


Fig. 3. Anatomical structures of *Liriodendron tulipifera*: (A to C) Light micrographs; (D to H) SEM images; Cross-sections (A, D) show vessel elements arranged in radial alignment; Radial surfaces (B, E to G) show homocellular rays composed of procumbent cells (E), heterocellular rays composed of procumbent cells and square marginal cells (F), perforation plates, either simple or scalariform, and vessel-ray pits rounded to angular, with much reduced to apparently simple borders (G); Tangential surfaces (C, H) show vessel elements with opposite inter-vessel pits (H); Scale bars: (A to C) = 200 μm ; (D to H) = 100 μm

In the quantitative analysis, the three diffuse-porous species showed significant differences in anatomical traits (Table 2). *B. platyphylla* exhibited the narrowest ARW, with an average of 2.33 ± 0.96 mm. However, this species had the longest vessel elements, with an average length of 931.61 ± 57.35 μm . *L. tulipifera* exhibited the widest fibers in the tangential direction (16.91 ± 2.51 μm) and the thickest fiber cell walls (4.32 ± 0.89 μm). Its vessel dimensions, including radial diameter (D_{rad} ; 71.59 ± 7.30 μm) and tangential

diameter (D_{tan} ; $53.80 \pm 7.21 \mu\text{m}$), were smaller than those of the other species. *Q. salicina* showed the widest ARW, with an average of $6.98 \pm 3.75 \text{ mm}$, and the thickest vessel cell walls ($3.20 \pm 0.24 \mu\text{m}$). Its vessel element length was shorter than that of the other species, with an average value of $320.42 \pm 32.96 \mu\text{m}$. Additionally, *Q. salicina* showed relatively small fiber dimensions, including radial diameter (D_{rad} ; $10.83 \pm 1.74 \mu\text{m}$) and tangential diameter (D_{tan} ; $7.72 \pm 1.12 \mu\text{m}$), as well as relatively thin fiber cell walls ($3.27 \pm 0.38 \mu\text{m}$).

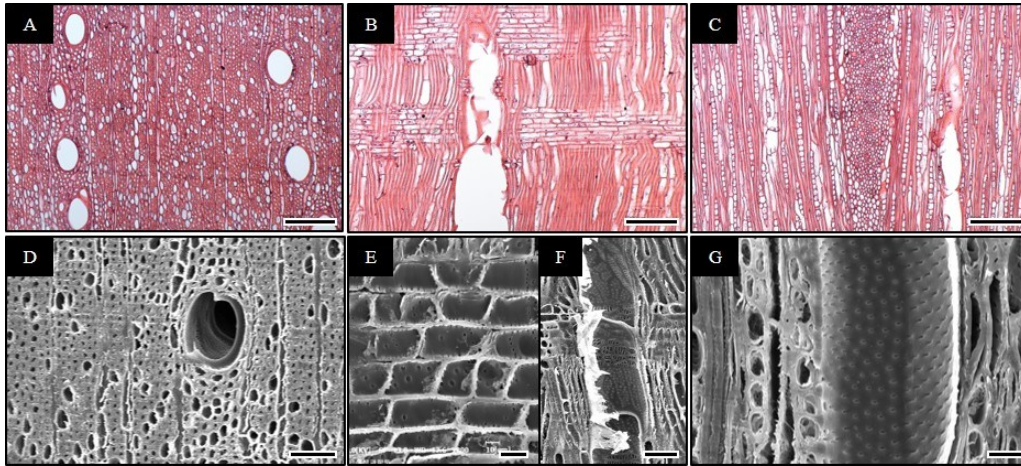


Fig. 4. Anatomical structures of *Quercus salicina*. (A to C) Light micrographs; (D to G) scanning electron micrographs (SEM). Cross-sections (A, D) show vessel elements arranged. Radial surfaces (B, E, and F) show rays composed of procumbent cells (E), simple perforation plates, and vessel-ray pits rounded to angular, horizontal (scalariform, gash-like) to vertical (palisade), with much reduced to apparently simple borders (F). Tangential surfaces (C, G) show vessel elements with alternate inter-vessel pits (G); Scale bars: (A to C) = $200 \mu\text{m}$; (D, F) = $100 \mu\text{m}$; (E, G) = $20 \mu\text{m}$

The predominance of radial multiples in *L. tulipifera* indicates a potentially higher degree of vessel-to-vessel contact compared with that of the other species. In contrast, *Q. salicina* is mainly characterized by solitary vessels, whereas *B. platyphylla* exhibits an intermediate condition with mostly solitary vessels and occasional radial multiples. Carlquist (2009) has emphasized that vessel distribution in wood is often nonrandom and may have functional significance, particularly in terms of conductive safety, mechanical organization, and water and photosynthate storage capabilities. Conductive safety is closely related to preventing or limiting xylem cavitation and the spread of embolism; thus, vessel arrangement may provide anatomical information relevant to hydraulic safety. However, because hydraulic conductivity and cavitation resistance were not measured in this study, the functional implications of these vessel arrangements should be interpreted with caution. Previous studies have reported contrasting interpretations of vessel groupings. Loepfe *et al.* (2007) predicted that enhanced vessel connectivity increased conductivity but reduced cavitation resistance by increasing the probability of embolism spreading. In contrast, Lens *et al.* (2011) found that enhanced vessel grouping in *Acer* was associated with increased cavitation resistance and reduced xylem area-specific conductivity. Therefore, the vessel arrangement patterns observed in this study are best interpreted as anatomical evidence of potential differences in xylem network organization rather than as direct evidence of hydraulic performance.

Table 2. Anatomical Traits of Three Diffuse-porous Hardwood Species

Anatomical Trait ^{1,4}	<i>B. platyphylla</i>		<i>L. tulipifera</i>		<i>Q. salicina</i>		Test used	F / χ^2 ⁵	df	p-value
	Mean (SD) ²	CV (%) ³	Mean (SD)	CV (%)	Mean (SD)	CV (%)				
ARW (mm)	2.33 (0.96) a	41.13	5.52 (2.38) b	43.11	6.98 (3.75) c	53.63	Kruskal–Wallis + Dunn (BH)	69.44	2	< 0.001
Fiber CWT (μm)	3.64 (0.38) b	10.31	4.32 (0.89) c	20.64	3.27 (0.38) a	11.65	Kruskal–Wallis + Dunn (BH)	33.69	2	< 0.001
Fiber width (D_{rad}) (μm)	17.59 (1.80) b	10.24	17.00 (3.65) b	21.46	10.83 (1.74) a	16.08	Kruskal–Wallis + Dunn (BH)	51.75	2	< 0.001
Fiber width (D_{tan}) (μm)	14.70 (1.68) b	11.41	16.91 (2.51) c	14.85	7.72 (1.12) a	14.56	Kruskal–Wallis + Dunn (BH)	65.21	2	< 0.001
Fiber length (μm)	1472.36 (126.12) b	8.57	1531.34 (94.83) b	6.19	1104.19 (79.89) a	7.24	ANOVA + Tukey HSD	154.16	2	< 0.001
Vessel CWT (μm)	1.79 (0.13) a	7.35	1.75 (0.27) a	15.65	3.20 (0.24) b	7.56	Kruskal–Wallis + Dunn (BH)	59.90	2	< 0.001
Vessel width (D_{rad}) (μm)	109.76 (8.79) b	8.01	71.59 (7.30) a	10.20	113.63 (9.86) b	8.68	ANOVA + Tukey HSD	213.36	2	< 0.001
Vessel width (D_{tan}) (μm)	82.23 (7.68) b	9.33	53.80 (7.21) a	13.40	84.81 (9.17) b	10.82	ANOVA + Tukey HSD	136.60	2	< 0.001
Vessel length (μm)	931.61 (57.35) c	6.15	731.76 (88.81) b	12.14	320.42 (32.96) a	10.29	Kruskal–Wallis + Dunn (BH)	77.32	2	< 0.001

¹ ARW, annual ring width; CWT, cell wall thickness; D_{rad} , width in the radial direction; D_{tan} , width in the tangential direction. ² Values are presented as mean (standard deviation, SD). Different letters following the SD indicate significant differences among species ($p < 0.05$). ³ CV, coefficient of variation, calculated as $(\text{SD} / \text{mean}) \times 100$. ⁴ For anatomical traits, $n = 30$ measurements per species. For ARW, $n = 64$ for *B. platyphylla* and *Q. salicina* and $n = 36$ for *L. tulipifera*. ⁵ F-values are reported for traits analyzed using one-way ANOVA followed by Tukey's HSD test, whereas χ^2 values are reported for traits analyzed using the Kruskal–Wallis test followed by Dunn's test with Benjamini–Hochberg (BH) correction.

Natural Durability of Three Diffuse-porous Wood Species

The natural resistance of *B. platyphylla* and *L. tulipifera* against wood-decaying fungi and termites has been examined in previous studies using the same samples (Jung *et al.* 2025). Therefore, the corresponding data were referenced in this study. The durability of *Q. salicina* was investigated in the present study, following the same procedures used in previous studies.

In the durability test against wood-decaying fungi, *B. platyphylla* exhibited the lowest resistance among the three diffuse-porous wood species, with the highest WL of $45.53 \pm 4.68\%$ (Fig. 5A). Although *Q. salicina* showed a greater WL ($40.24 \pm 4.12\%$) than *L. tulipifera* ($35.95 \pm 5.73\%$), the difference was not statistically significant (Tukey's HSD, adjusted $p = 0.126$; Fig. 5A).

In the termite resistance test, clear differences in termite resistance were observed among the three wood species (Fig. 5B). *B. platyphylla* showed the lowest resistance, with the highest WL of $40.32 \pm 1.60\%$, which was consistent with its low resistance to wood-decaying fungi. In contrast, *L. tulipifera* exhibited the highest resistance to termite attack, resulting in a significantly low WL of $1.76 \pm 0.33\%$ (Fig. 5B). *Q. salicina* showed moderate termite resistance among the species tested, with a WL of $11.48 \pm 2.93\%$ (Fig. 5B).

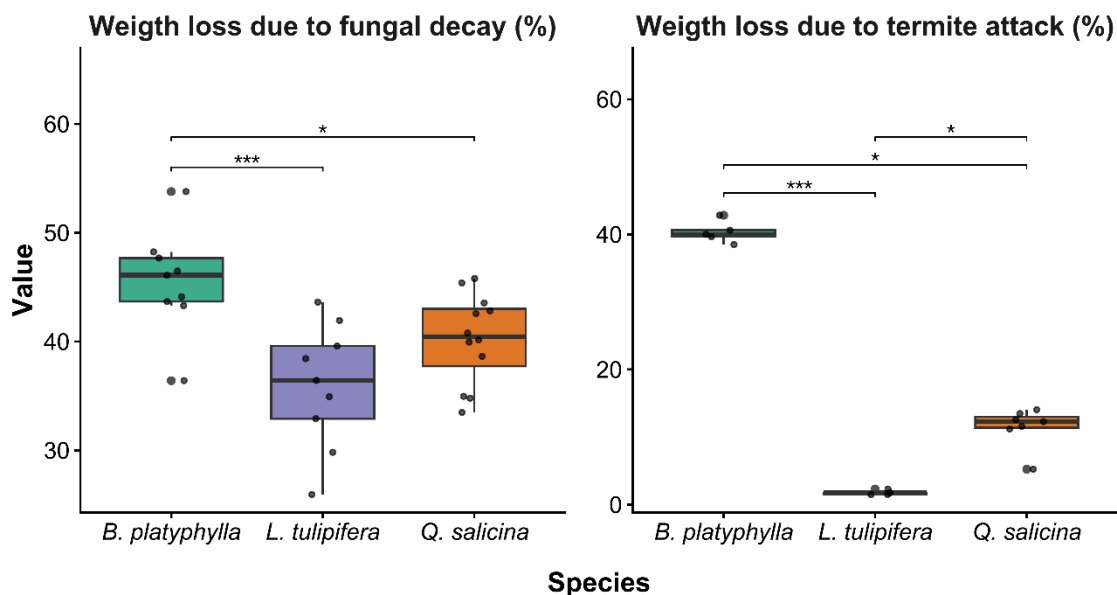


Fig. 5. Natural durability of three diffuse-porous wood species: (A) Weight loss (%) due to fungal decay; (B) Weight loss (%) due to termite attack; Boxplots show the median and interquartile range, with individual data points overlaid (jittered for clarity); Asterisks (*) indicate significant differences (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$): (A) based on Tukey's HSD test following one-way ANOVA; (B) based on Dunn's test with Benjamini–Hochberg correction following the Kruskal–Wallis test. For the fungal decay test, $n = 12, 9$, and 12 for *B. platyphylla*, *L. tulipifera*, and *Q. salicina*, respectively; for the termite resistance test, $n = 5, 5$, and 7 , respectively

Representative images of the specimens after the termite resistance test are shown in Fig. 6A. In *B. platyphylla*, clear evidence of severe termite attack was observed, including tunnel formation and extensive feeding damage. In *Q. salicina*, moderate to severe damage, including penetration of the wood surfaces, was detected. In contrast, *L.*

tulipifera showed little to no visible evidence of termite attacks, and the damage was negligible or absent.

Termite mortality and visual assessments further supported these results (Fig. 6B). *B. platyphylla* exhibited a low termite mortality rate of $13.9 \pm 3.2\%$ and a visual rating of 4.9 ± 1.2 , indicating low resistance (the mortality of termites in the control vessel is $13.9 \pm 3.2\%$). Conversely, *L. tulipifera* demonstrated exceptionally high resistance, with a mortality rate of $99.2 \pm 0.9\%$ and a visual rating of 9.4 ± 0.3 . *Q. salicina* again showed moderate resistance, with a mortality rate of $50.5 \pm 10.4\%$ and a visual rating of 7.8 ± 0.7 .

To the best of the authors' knowledge, this is the first study to provide information on the natural durability of *Q. salicina* against wood-decaying fungi and subterranean termites. Its resistance to fungal decay was not significantly different from that of *L. tulipifera*. Concurrently, *Q. salicina* exhibited substantially greater termite resistance than *B. platyphylla*. These findings provide baseline durability data for *Q. salicina*.

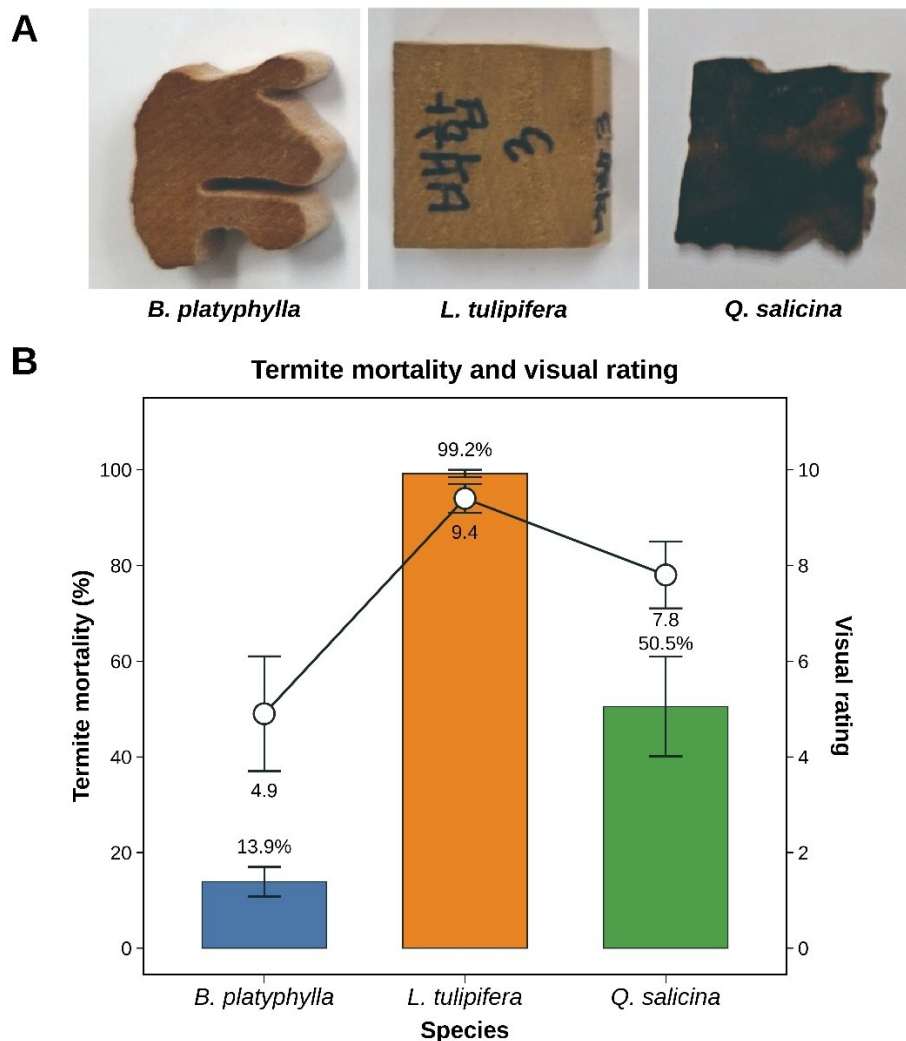


Fig. 6. Results of the durability test against termites: (A) Representative appearance of wood specimens after termite exposure; (B) Termite mortality and visual rating based on AWP E1-17 (AWPA 2017). Values are presented as mean $\pm$ standard deviation (SD; $n = 5$ for *B. platyphylla* and *L. tulipifera* and $n = 7$ for *Q. salicina*)

Multiple Factor Analysis of Diffuse-porous Wood Species

MFA was conducted on the species-level mean values of the three diffuse-porous hardwood species examined to explore patterns of multivariate association among anatomical characteristics, ARW, and WL by fungal decay and termite attack.

Given the small number of species, the analysis was exploratory, and the observed multivariate associations should be interpreted with caution, not as statistically robust or broadly generalizable relationships. The first two dimensions accounted for the total variation in the dataset, with MFA1 and MFA2 accounting for 70.4% and 29.6% of the variation, respectively (Fig. 7A). The WL due to termite attacks and WL due to fungal decay contributed most strongly to MFA1, accounting for 33.2% and 30.1% of this dimension, respectively, followed by ARW (28.8%). Anatomical traits contributed relatively little to MFA1 (7.9%). In contrast, MFA2 was dominated by anatomical traits, which accounted for 79.5% of the variation in MFA2, whereas ARW, WL due to fungal decay, and WL due to termite attack contributed 11.2%, 8.3%, and 1.0%, respectively. These results suggested that durability-related variables and ARW were primarily represented by MFA1, whereas anatomical variation was primarily expressed by MFA2.

The MFA biplot illustrates the distinct positioning of the three species within the multivariate trait space (Fig. 7B). *B. platyphylla* was positioned on the positive side of MFA1, relatively close to the vectors for WL caused by fungal decay and termite attack. *L. tulipifera* was located in the lower-left region of the ordination space, near the fiber CWT vector, whereas *Quercus salicina* was located in the upper-left region, near ARW and vessel CWT. Anatomical variables, including vessel and fiber characteristics, were distributed primarily along MFA2, indicating that anatomical variation represented a major secondary axis for species differentiation.

Exploration of the variable vectors further suggested that the associations between WL due to fungal decay and anatomical traits varied among anatomical features. The WL due to fungal decay was oriented in a direction similar to that of vessel radial and tangential widths, whereas fiber CWT was positioned in the opposite quadrant of the ordination space. Vessel CWT and ARW were also separated from the WL due to fungal decay vector. Simultaneously, fiber radial and tangential widths, fiber length, and vessel length were distributed toward the lower-right region. Thus, among the measured anatomical variables, vessel width appeared to show the closest association with WL due to fungal decay, whereas fiber CWT exhibited an opposing orientation within the ordination space. In comparison, WL due to termite attacks was oriented predominantly along MFA1 and showed limited alignment with anatomical trait vectors.

At the individual variable level, fiber tangential width (12.0%), fiber length (11.5%), fiber CWT (11.2%), and vessel CWT (10.7%) were among the strongest contributors to MFA2, with fiber radial width (9.82%), vessel radial width (8.66%), and vessel tangential width (8.57%) contributing appreciably (Fig. 7C). Although vessel width variables were not the largest contributors to MFA2, their vector orientations were most similar to the orientation of WL due to fungal decay in the MFA biplot. In contrast, fiber CWT contributed strongly to MFA2 but was positioned in the quadrant opposite to that of WL due to fungal decay. These variable-level contributions provide additional context for the contrasting spatial patterns of WL caused by fungal decay and the anatomical traits observed in Fig. 7B. The WL due to termite attack contributed only marginally to MFA2, which is consistent with its limited correspondence with the anatomical trait vectors in the biplot.

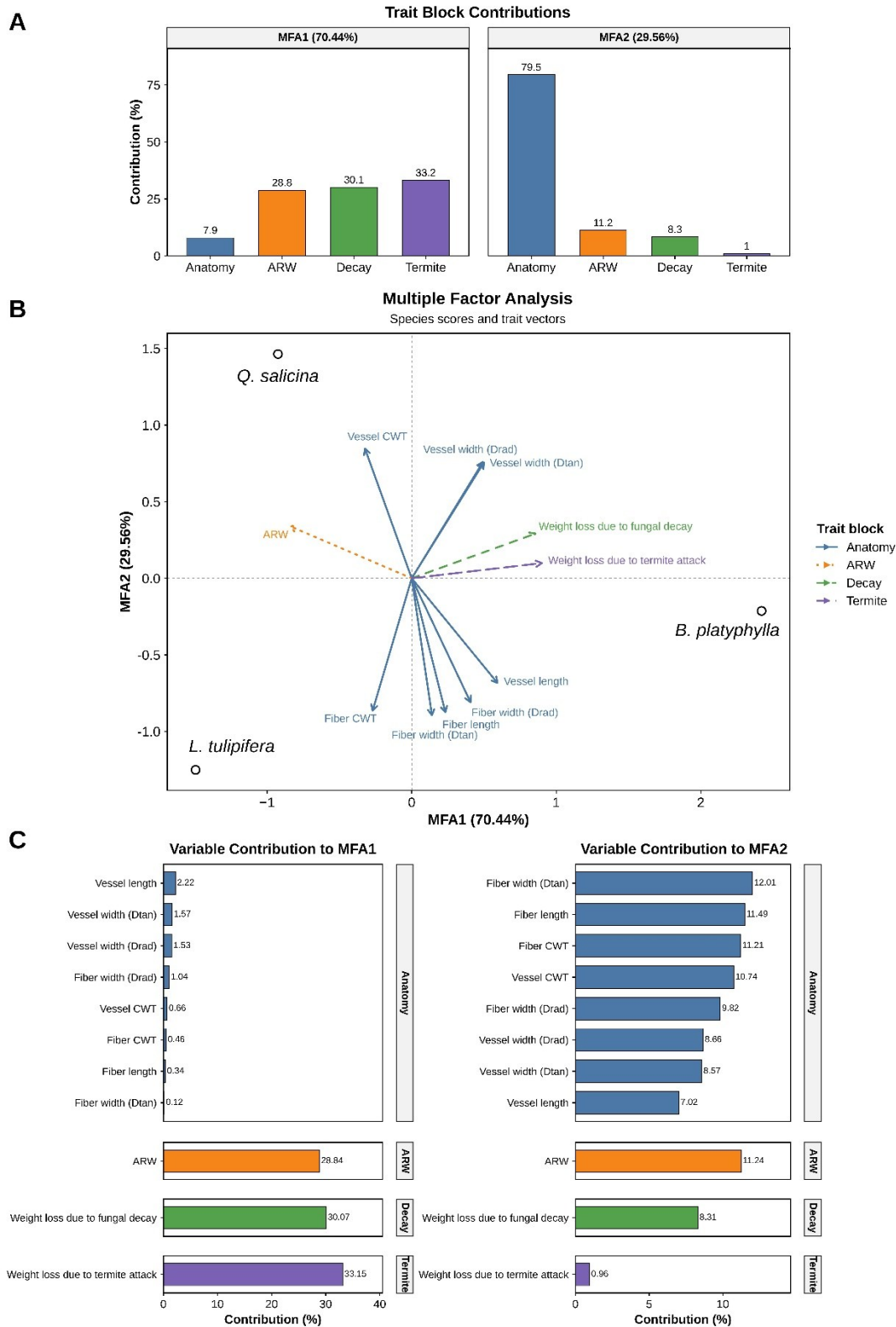


Fig. 7. MFA of wood anatomical traits, ARW, WL due to fungal decay, and WL due to termite attack: (A) Trait block contributions to MFA1 and MFA2; (B) MFA biplot showing species scores and trait vectors; (C) Variable contributions to MFA1 and MFA2 for each trait block

Association of Anatomical Traits and Natural Durability

Previous studies have suggested that wood anatomy influences fungal colonization by affecting moisture distribution, permeability, lumen connectivity, and the accessibility of wood tissues to fungal hyphae (Daniel 2003; Schwarze 2007). In particular, the relative proportions and dimensions of vessels and fibers are associated with differences in moisture dynamics and fungal penetration pathways, which may ultimately influence decay susceptibility. In the present study, several quantitative anatomical traits provided useful insight into variation in fungal decay resistance among the examined diffuse-porous hardwoods.

Among the examined species, *L. tulipifera* exhibited the lowest fungal weight loss and was distinguished by its relatively thick fiber walls and small vessel dimensions. In contrast, *B. platyphylla*, which showed the greatest fungal weight loss, possessed relatively long vessel elements and less pronounced fiber wall development than *L. tulipifera*. These contrasting characteristics suggest that the anatomical structures are associated with some of the observed variations in fungal decay resistance. A relatively high proportion of cell wall material and small conducting elements may reduce the continuity of the lumen space available for fungal spread and influence moisture movement within wood tissues. In contrast, relatively large or elongated conducting elements may facilitate the longitudinal movement of moisture and fungal hyphae.

However, the documented relationships were not consistent across all species. For example, *Q. salicina* possessed relatively thick vessel walls but showed intermediate weight loss due to fungal decay, indicating that CWT alone could not account for decay resistance. Similarly, the vessel element length and fiber dimensions varied among species; however, their relationship with fungal decay resistance was not straightforward. The MFA results were generally consistent with this interpretation, showing an exploratory alignment between fungal weight loss and certain anatomical characteristics, particularly vessel width. Given the small number of species examined, however, this pattern should not be interpreted as evidence of a direct or causal relationship.

The relationship between anatomy and termite resistance was even less evident. Although *L. tulipifera* differed from the other species in vessel width and fiber-wall thickness, these traits could not explain its near-complete termite resistance. The measured vessel and fiber traits were insufficient to explain this response, suggesting that the anatomical traits examined in this study cannot fully account for termite resistance. These findings are consistent with those of previous studies, indicating that natural durability is governed by a complex combination of anatomical, physical, and chemical properties rather than by wood structure alone (Taylor *et al.* 2002).

Overall, the results suggest that certain anatomical traits, particularly vessel dimensions and fiber wall development, are associated with variations in fungal decay susceptibility among diffuse-porous hardwood species. However, no single anatomical characteristic consistently explained the durability patterns observed among the three species examined in this study. Anatomical traits alone accounted for only part of the variation in natural durability, particularly in termite resistance.

Limitations and Future Research

Several limitations should be considered when interpreting these results. First, only one tree was sampled for each species, and the three trees came from different geographic locations. Consequently, species, individual-tree, and site effects cannot be fully separated, and the observed differences should not be interpreted as population-level differences

among the three species. Future studies should sample several trees per species across multiple sites to determine whether the observed patterns are reproducible.

Second, we did not measure chemical or physical wood properties, in particular the content and composition of heartwood extractives, such as phenolics, tannins, flavonoids, quinones, and terpenoids, which are known to influence resistance to fungal decay and termite attack (Schultz and Nicholas 2000; Dickson *et al.* 2007; Kirker *et al.* 2013; Nascimento *et al.* 2013). Other properties, including moisture dynamics, permeability, density, chemical composition, and the spatial distribution of extractives, may also influence natural durability (Brischke and Rapp 2008; Meyer-Veltrup *et al.* 2017; Brischke and Alfredsen 2020; De Ligne *et al.* 2020; Martín and López 2023; Kirker *et al.* 2024). Therefore, the associations between anatomy and durability identified here cannot be separated from the potential effects of these unmeasured properties. Moreover, because the MFA was based on species-level means from only three species, the observed multivariate associations should be regarded as exploratory rather than statistically robust or broadly generalizable. Future studies integrating anatomical, chemical, and physical properties across more species, with independent biological replicates, are needed to determine the relative contributions of these properties to natural durability.

Finally, fungal decay resistance was evaluated only by weight loss. Although weight loss is widely used as an indicator of fungal decay, it may not fully capture fungal colonization or the structural and chemical changes that occur during the early stages of decay, before mass loss becomes measurable. The fungal decay results should therefore be interpreted as mass loss under the experimental conditions rather than as a comprehensive measure of all stages of fungal degradation. Future studies could supplement weight loss with other indicators of fungal colonization and wood degradation.

CONCLUSIONS

1. Whether readily measurable anatomical characteristics could serve as indicators of the natural durability of three diffuse-porous hardwood species in Korea was evaluated. The results showed that fungal decay resistance was associated with certain anatomical traits, particularly vessel-related characteristics. In contrast, termite resistance exhibited a relatively weak correlation with the measured anatomical variables. These findings suggest that anatomical characteristics contribute to variation in fungal decay susceptibility among the three species examined in this study but do not consistently explain natural durability.
2. This study provides baseline information on the anatomical characteristics and natural durability of the three major diffuse-porous hardwood species in Korea. The results indicate that anatomical traits alone are insufficient to explain durability variation and should be considered together with physical and chemical wood properties. These findings are limited to the three species examined and should not be generalized to other species. Further studies integrating anatomical, physical, and chemical datasets across a broader range of species are needed to determine whether the observed patterns apply more broadly and to improve our understanding of the mechanisms underlying natural durability.

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Conflict of Interest

The authors declare that there are no conflicts of interest.

Use of Generative AI

Generative AI was not used in the preparation of this manuscript.

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