A TYPOLOGY OF VESSEL PATTERNING IN TREES WITH EXAMPLES FROM THE FOSSIL RECORD

D. W. Woodcock1,*

*Marsh Institute, Clark University, 950 Main Street, Worcester, Massachusetts 01910, USA

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Premise of research. The diversity of anatomical features in wood presents a challenge for understanding wood functioning and developing fossil wood as a paleoenvironmental proxy. This study focuses on the variation in vessel-related features in trees to identify environmental correlates and address questions relating to function and adaptation.

Methodology. The features considered include vessel diameter and density; the occurrence, degree, and type of vessel grouping; the variable vessel diameter seen in some woods; and vessel arrangements of various types. Starting from the question of the basic or most typical type of vessel patterning in the midlatitudes versus the tropics, the analysis employs midlatitude/tropical comparisons, information in online databases, examples of modern and fossil woods, and novel ways of representing vessel patterning as a basis for interpretation.

Pivotal results. A typology is presented that illustrates the range of variation in vessel patterning in trees and shows both temperature-related disjunctions between the tropics and the midlatitudes and the influence of moisture availability. The diffuse-porous woods of the tropics have a wide range of vessel diameters and densities, whereas in the midlatitudes, diffuse-porous woods have vessels only in the narrow-diameter, high-density categories and ring-/semi-ring-porous woods are also present. The posited relationship between vessel diameter and height is not so clear for the floras considered, especially for tall forest trees. Woods with variable vessel diameters are quite diverse; the complex patterns in some Eocene fossil woods may reflect increased water stress during a time of global warmth.

Conclusions. Variation in vessel patterning shows clear relationships to climate and environment that can be used in interpreting paleoenvironments. However, understanding adaptive pathways requires consideration of a broader range of anatomical features and functional and developmental constraints.

Keywords: vessel diameter and density, vessel diameter and distribution plots, wood anatomy, fossil wood, Piedra Chamana fossil forest (Peru).

Introduction

This study deals with vessel diameter and density and the patterns associated with variation in these features in angiosperm trees. The first question addressed is what might be considered the most basic vessel pattern and the way that this differs in the midlatitudes and tropics. A secondary question is what is the most common patterning in these areas. Following from this, I examine different aspects of vessel patterning and relationships to habit and environmental factors. Examples are drawn from modern tropical and midlatitude woods, in particular those in tropical South America and temperate North America, and an Eocene assemblage of fossil woods from South America (Woodcock et al. 2009, 2017, 2019; Woodcock and Meyer 2020). Geographical comparisons also rely on information in the InsideWood (2004−) database (Wheeler 2011); the approach taken is similar to that of Wheeler et al. (2007), who used the InsideWood database to survey geographical variation across a range of wood characters but looked at woody plants in general and compared geographical regions different from those considered here. Reasons for referencing fossils are the large number of fossil woods described (~1200 taxa in the InsideWood database; InsideWood 2004−), the studies that have been made on variation in wood anatomical characteristics over geologic time (Wheeler and Baas 2019) and vessel patterning in fossil woods (Woodcock and Meyer 2020), and interest in fossil wood as a source of information about past climates and...
environments (Wiemann et al. 2001; Martínez-Cabrera and Estrada-Ruiz 2018, 2021). The typology shows the range of variation in character space and provides a framework for looking at the diversity of wood structure, relationships to climate and the environment, and interrelationships among features important for understanding adaptive pathways.

**Material and Methods**

Examples of wood types from the InsideWood (2004–) database are considered representative of certain forest types, wood anatomical functional types, or regions and are also ones for which photomicrographs at a standardized scale were available. Additional examples are from the Piedra Chamana fossil woods, a late Middle Eocene (39 Ma) assemblage of fossil woods and leaves representing lowland tropical forest (Woodcock et al. 2009, 2017, 2019; Woodcock and Meyer 2020). Information about ranges and tree stature is from Elias (1980), the Tropical Plants Database (Fern 2018), and the Global Biodiversity Information Facility (GBIF 2020). InsideWood (2004–; Wheeler 2011) is also used as a source of information and analytical data. The InsideWood database includes information at both the species and genus level and additionally sometimes also includes duplicate listings; thus, the percentages calculated give only a general idea of occurrences. Most comparisons are for New World forests, specifically in North America north of Mexico and tropical South America (comprising South America north of 20°S). Tropical South America is within the “Neotropics and temperate Brazil” region (also including Mexico and Central America, the Caribbean, and southern Brazil) used in the comparative analysis of Wheeler et al. (2007). In the InsideWood database, characters can be indicated as present or variably present, information that is used in some cases to provide an idea of the range of values present or uncertainty relating to determinations. Anatomical characterizations and terminology conform to International Association of Wood Anatomists (IAWA) guidelines (IAWA Committee 1989) except where indicated. For the vessel diameter and distribution plots and diameter distributions, all vessels were measured within a 4-mm-wide area up to a total of 60 vessels, and the distributions were tested for nonnormality using the Shapiro-Wilk test (Woodcock and Meyer 2020).

**On the Question of What Is a Basic or Typical Wood Type in Trees in the Midlatitudes and Tropics**

The first question addressed is whether it is possible to characterize those woods with the simplest/most basic type of vessel patterning in the midlatitudes and tropics. The areas considered are North America north of Mexico and tropical South America, regions coded in the InsideWood database. A secondary question is what could be considered a typical type of vessel patterning in these two areas. I focus on areas where conditions are most favorable for the growth of trees, specifically, the eastern deciduous forest region of North America, where temperatures fall below freezing but precipitation is evenly distributed throughout the year, and the South American lowland tropical forest region, a frost-free area supporting broad-leaved evergreen or mixed evergreen deciduous forest. In the InsideWood (2004–) database, tropical South America (comprising South America north of 20°S) encompasses a range of lowland tropical forest types as well as montane associations; however, trees in megadiverse lowland tropical forests predominate numerically in the database.

**Midlatitudes**

Generally, the simplest type of vessel patterning is seen in the diffuse-porous woods. In these woods, vessel diameter does not vary significantly. Six examples from the North American eastern deciduous forest are shown in figure 1. All have growth rings, vessel diameters in the low-intermediate category (50–100 μm), and vessel frequencies ≥20 mm⁻² (InsideWood 2004–). For diffuse-porous trees in North America north of Mexico (except in tropical Florida), 30–100 μm is the upper limit for vessel diameter and vessel densities less than 20 mm⁻² do not occur (InsideWood 2004–). One of the woods (fig. 1A) has solitary vessels—feature 9, “vessels exclusively solitary (90% or more),” in the IAWA Committee (1989, p. 242) coding system—a character occurring in ~11% of diffuse-porous trees in North America north of Mexico (~13% of all diffuse-porous tree taxa; InsideWood 2004–). Two woods have vessels that are solitary and in radial multiples of two to four (fig. 1B, 1C), the default condition in the IAWA coding system, with a prevalence of ~70% in trees (81% of diffuse-porous trees; InsideWood 2004–; Wheeler et al. 2007). Three woods display vessel groupings—feature 10, “vessels in radial multiples of 4 or more common” (fig. 1D), or feature 11, “vessel clusters common” (IAWA Committee 1989, p. 242; fig. 1E, 1F). Vessel groupings occur at a frequency of 18% in North America north of Mexico (6% of diffuse-porous trees). Some of these woods also show variation in vessel diameter and density not pronounced enough to be considered semi-rings-porous (fig. 1B) or a region at the end of the growth ring with fewer vessels (fig. 1E, 1F).

These six diffuse-porous trees are deciduous and have broad ranges in the eastern United States. Five are canopy trees, including two of the tallest trees in the eastern forests—Liquidambar styraciflua, up to 40 m, and Liriodendron tulipifera, up to 30–50 m (Elias 1980). One (Corns florida) is a subcanopy tree (up to 15 m). Trees with diffuse-porous wood are the most important elements in some riverine (Plat anus L.) or freshwater swamp (Acer rubrum) environments, are dominant species in the riparian/bottomland flora, and include important mesic forest trees (Acer L. and Betula L. species). Liriodendron L. (a magnoliid), Plat anus L. (Proteales), and Liquidambar L. (Altingiaceae) have a fossil history extending to the Cretaceous (Stevens 2001–) and wood characteristics—scalariform perforations, at least in latewood vessels, and scalariform or opposite intervessel pitting (Brown and Panshin 1940; InsideWood 2004–)—that have been considered less derived, have declined in prevalence in the midlatitudes since the Late Cretaceous and Paleocene, and have been infrequent in the tropics since the Cretaceous (Wheeler and Baas 2019). The prevalence of scalariform perforations in moist forest and riparian habitats and their association with increased flow resistance are consistent with the idea that this feature is selected against where there is significant water stress (Carquist 2012, 2013; Wheeler and Baas 2019).
Diffuse-porous wood is not, however, the most typical wood type in the eastern deciduous forest since many forest trees are ring- or semi-ring-porous. Important genera include ring-porous *Quercus* L. (25-plus deciduous species), *Carya* Nutt., *Ulmus* L., *Fraxinus* L., and *Celtis* L.; semi-ring-porous *Aesculus* L. and *Juglans* L.; and variably semi-ring-porous *Prunus* L. and *Salix* L. In contrast, *Acer*, *Betula*, and *Tilia* L. (totaling 15 species) are the most important diffuse-porous genera. And even in alluvial/lowland forests where diffuse-porous trees are particularly important, they are generally associated with ring- or semi-ring-porous Fraxinus, Juglans, and Quercus species. Thus, while diffuse-porous wood with vessels 50–100 μm and ≥ 20 mm² that are ungrouped is the most basic type of vessel patterning in eastern deciduous forest trees and is found in trees that are dominants in some types of environments, this wood type cannot be considered the most typical of the region because of the prevalence of ring and semi-ring porosity.

**Tropics**

Diffuse-porous wood is prevalent in the tropics and is found in trees both with and without visible growth rings. Representative examples from tropical South America are shown in figure 2. These tropical woods have a wide range of vessel diameters and densities. Categorical data (InsideWood 2004—) show that the high-intermediate vessel diameter category (mean

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![Transverse sections of diffuse-porous woods from eastern North America.](image-url)
tangential diameter 100–200 μm”; IAWA Committee 1989, p. 258) and next to lowest vessel density category (“5–20 vessels per square millimetre”; IAWA Committee 1989, p. 259) are most common (fig. 2B, 2E, 2F). Three woods (fig. 2B, 2C, 2E) have “vessels exclusively solitary (90% or more)” (IAWA Committee 1989, p. 242). As in the midlatitudes, exclusively solitary vessels are uncommon, occurring in 10% of diffuse-porous trees in tropical South America (InsideWood 2004–). Five woods have vessels that are solitary and in short multiples (fig. 2A, 2D, 2G, 2H). This default category occurs in 85% of tropical South American trees. None has grouped vessels—“vessels in radial multiples of 4 or more common” or “vessel clusters common” (IAWA Committee 1989, p. 242). Vessel grouping is less common than in North America north of Mexico, occurring in ~5% of trees (InsideWood 2004–). Thus, in the South American tropics, the simplest vessel patterning (diffuse-porous woods with vessels that are solitary or solitary and in short multiples) encompasses a broad range of vessel diameters and densities, and the most typical patterning in climates with abundant rainfall is seen in diffuse-porous woods with vessels that are solitary or solitary and in short multiples, 100–200 μm in diameter, and 5–20 mm⁻².

Aspects of Vessel Patterning

Vessel Diameter

Vessel diameter ranges over an order of magnitude in woody plants, variation that can be related to both stature (e.g., shrubs vs. trees) and vegetation type (woodland vs. forest). Increasing vulnerability to embolism with increasing diameter where there is water stress or temperatures fall below freezing is a basis for understanding limits on vessel diameter imposed by climate (Hacke et al. 2017; Venturas et al. 2017). On the other hand, geophysical considerations—specifically, the advantage of having narrow distal conduits in the leaves, the increase in hydraulic resistance with length in constant-diameter conduits, and the consequent biophysical advantage of having basal vessel diameter increase with increasing stem length—have been advanced as indicating the importance of height or stature as a determinant of vessel diameter (Olson et al. 2014, 2018). Studies demonstrating relationships to climate include that of Pfautsch et al. (2016), who found a significant relationship with potential evaporation across an aridity gradient in *Eucalyptus* L’Hér when height is controlled for. However, broader surveys have generally shown the greater

![Fig. 2](image-url) Diffuse-porous woods from tropical South America. A, *Maytenus obtusifolia* Mart. (PACw.S1.1290), vessels solitary and in short multiples. B, *Calophyllum brasiliensis* Cambess. (J.A.Wolfe 477), vessels solitary. C, *Guaiacum officinale* L. (Kw.25858), vessels solitary. D, *Coccoloba echinata* Lam. (Kw.SF797E), vessels solitary and in short multiples. E, *Licania hypoleuca* Benth. (FH2w.8251.xa), vessels solitary. F, *Inga velutina* Wild. (T.D.Pennington_12447), vessels solitary and in short multiples. G, *Dalbergia nigra* (Vell.) Benth. (PACw.7391), vessels solitary and in short multiples. H, *Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels (USw.30793), vessels solitary and in short multiples. Scale bars = 200 μm. Photos: A, B, E–H courtesy of E. Wheeler, North Carolina State University; C, D courtesy of P. Gasson, Royal Botanic Gardens, Kew (InsideWood 2004–).
importance of height (Fichtler and Worbes 2012; Morris et al. 2018; Olson et al. 2018). Fichtler and Worbes (2012), in a study of 111 species of tropical trees, found higher correlations to height and a significant difference among height classes. Olson et al. (2018), in a study of >500 species across eight vegetation zones, also found that the most important explanatory variable was height (or stem length since lianas were also included); a follow-up study (Olson et al. 2020) looked at other influencing factors, including porosity type and the presence of scalariform perforation plates.

The analysis of Olson et al. (2018) includes a site in the North American eastern deciduous forest in Connecticut (mesophytic forest region of Dyer [2006]; lat. 41.953°N, long. −72.122°E). A plot of vessel diameter versus stem length for the 29 species sampled is shown in figure 3A. The relationship between vessel diameter and length shows considerable scatter (and is nonsignificant) for trees of >15 m. The gap in stem length in the middle range is consistent with other mature temperate forests (King et al. 2006), which tend to have a diversity of tall forest tree species and a less diverse subcanopy component (the data include shrubs and herbs). Of trees with stem lengths of >15 m, diffuse-porous taxa generally fall below and ring-porous taxa above the regression line. The diffuse-porous trees include *Liriodendron* (DP5 in fig. 3A), one of the taxa shown in figure 1. IAWA guidance (IAWA Committee 1989) is to measure only the wider vessels of ring-porous woods and to sample vessels along a radial transect in the case of semi-ring-porous woods. If vessels are measured in this way instead of averaged, there would be an even greater difference between the ring- and diffuse-porous taxa. One ring-porous outlier among the shorter trees is *Sassafras albidum* (Nutt.) Nees (RP5 in fig. 4A). This species, the widest vessels of which are up to 120–160 µm (Brown and Panshin 1940), tends to be shrubby or short in the northern part of its range, which includes Connecticut, but grows taller (up to 30 m) farther south and on good sites (Griggs 1990). This example shows how wood characteristics can reflect adaptation to a niche that may not be available or realized in all parts of a range.

The Olson et al. (2018) database includes a Neotropical forest in Mexico (Los Tuxtlas in Veracruz; lat. 18.577°N, long. −95.080°E). This plot (fig. 3B) also shows a greater degree of scatter for taller trees (and a nonsignificant relationship for trees of >15 m). An outlier among the taller trees is *Liquidambar styraciflua*, one of the relatively narrow-vasseled (50–100 µm in diameter) diffuse-porous taxa (fig. 1) of the eastern deciduous forest, occurring here in a disjunct part of its range. Another (*Wimmeria bartlettii* Lundell) is in a family (Celastraceae) in which vessels tend to be narrow (except in lianas). Other examples of lowland tropical forest canopy trees with narrow vessels (50–100 µm) are *Maytenus obtusifolia* (Celastraceae; fig. 2A), up to 30–32 m; *Aspidosperma excelsum* Benth. (Apocynaceae), up to 30 m; and *Calycophyllum spruceanum* (Benth.) Hook.f. ex K Schum (Rubiaceae), up to 25–30 m (InsideWood 2004; Fern 2018). These three families tend to be shrubs or small trees but include some species that are canopy entrants.

Other outliers for trees of >15 m in figure 3B are two with vessels in the widest diameter class (≥2000 µm): *Ceiba pentandra* (L.) Gaertn, 30 to ~60–70 m, and *Ficus insipida* Willd., up to 40 m (Fern 2018). Both have abundant axial parenchyma—diffuse-in-aggregates parenchyma in *C. pentandra* and wide parenchyma bands in *F. insipida*. Morris et al. (2018) looked at factors with a possible influence on vessel diameter and found that the best explanatory model included the presence/extent of axial parenchyma, maximum tree height, and mean annual temperature. Wider vessels were associated with the presence of well-developed paratracheal (vessel-associated) parenchyma and also apotracheal diffuse-in-aggregates and banded parenchyma; aliform-confluent paratracheal and widely banded parenchyma are more common in the tropics than in temperate areas (Wheeler et al. 2007). Two other taxa that have wide vessels and are “highly parenchymatous” (Carlquist 2013) are...
Carica papaya L. and Jacaratia dolichaula (Donn.Sm) Woodson (both Caricaceae), distinctive short-statured pachycaul trees characterized as stem-succulent species in which mechanical support is linked to the development of a thick water-filled (parenchymatous) trunk (Carlquist 1998; Chapotin et al. 2006).

It is also instructive to look at vessel diameter in tall emergent trees. In the eastern deciduous forest, these are the magnoliid Liriodendron styraciflua and the conifer Pinus strobus L., reaching heights of 40–45 m or more (Burns and Honkala 1990).

Liriodendron, with vessels 50–100 μm, is a pioneer species persisting as an emergent element in mesic forests; P. strobus, with even narrower conductive elements (tracheids), is likewise a long-lived early successional tree. In tropical South America, lowland tropical forests have a canopy height of ~35–40 m, with emergents up to ~65 m. Information about the tallest Neotropical trees is incomplete, but of nine taxa known to reach heights of 50–60 m (Gorgens et al. 2019; Scipioni et al. 2019), four have a vessel diameter averaging or ranging up to >200 μm (C. pentandra, Caryocar villosum (Aubl.) Pers., Anacardium occidentale L., Bertholletia excelsa Bonpl). Conversely, tropical South American trees with an average vessel diameter of ≥200 μm (IAWA characters 43, 186, and 189, with 42 absent), numbering ~90, are mostly medium-sized canopy or emergent trees (mainly Caryocaraceae, Chrysobalanaceae, Lecythidaceae, Malvaceae-Bombacoideae, Vochysiaceae, and some legumes). But also included are shorter-statured trees appearing to be either (a) variably semi-ring-porous (Cordia species, Cordiaceae) or (b) in genera with abundant axial parenchyma and that also include tall tree species (Erythrina fusca Lour., Papilionoideae; Ceiba insignis (Kunth) P.E.Gibbs & Semir, Bombacoideae).

Vessel diameter has been considered among the more plastic aspects of wood structure—and by extension more likely to respond to variations in climate or habit—because it is not constrained by the length of the fusiform cambial initials (Carlquist 2013). However, studies demonstrating close relationships between vessels and the parenchyma fraction (Carlquist 2018; Morris et al. 2018) argue for a view of wood structure in which vessel diameter is closely integrated into the general adaptation of wood to the environment and thus subject to a range of anatomical and functional constraints. Shoot length may be an important driver of variation in vessel diameter in an evolutionary sense, but this does not appear to be a tightly constrained relationship functionally in trees in general. In the midlatitudes, it is not the case that the tallest trees have wide vessels, although wide vessels are limited to tall trees (or lianas). And in the tropics, not only do tall trees not necessarily have wide vessels, but wide-vesseled woody plants are not necessarily tall.

Fig. 4 Vessel diameter and density categories for diffuse-porous woods. A, North America north of Mexico (InsideWood feature 183/Brazier and Franklin category 80; n = 185). B, Tropical South America (InsideWood feature 186; n = 2325). Diffuse-porous woods predominate in the tropics but represent only a portion of temperate North American woods. Numbers in red indicate the percentages of occurrence. Data are from InsideWood (2004–).
Vessel Density

Vessel density (discussed only with respect to diffuse-porous woods) can range to as low as 1 mm⁻² in some tropical trees. The IAWA feature list uses five categories with end members of ≤5 and ≥100 mm⁻². Vessel density ≥100 mm⁻² occurs in only 3%–7% of trees and is more common in shrubs, with values of >500 mm⁻² occurring in shrubs in desertic or alpine environments (Carlquist and Hoekman 1985; InsideWood 2004–). Whereas vessel diameter is generally seen as coupled to water need in the leaves and thus is directly related to physical constraints such as height, water stress, and other factors affecting water transport, vessel density has been related to redundancy in the transport system (Carlquist 2013). An inverse relationship between vessel diameter and density has often been noted and may be affected by constraints related to packing of the vessels and the need for living tissue (parenchyma) and fiber/fibriform fractions (Carlquist 2012). However, this relationship is not strong (Fichtler and Worbes 2012), and Carlquist (2013) considers that vessel density is at least in part a measure of the degree of xeromorphy/mesomorphy and thus is linked to climate and environmental factors. But as with vessel diameter, stature has an influence, as is seen in the higher values in shrubs (modal vessel density category of ≥100 mm⁻² for trees and 40–100 mm⁻² for shrubs in North America north of Mexico; InsideWood 2004–).

Vessel Diameter and Density Considered Together

The variability of vessel diameter and density in trees with diffuse-porous wood can be represented using categorical data (fig. 4). The plots show the nonoccurrence of sparse-narrow and dense-wide vessels. Midlatitude woods occupy a narrow part of character space at the dense-narrow end of the spectrum. Tropical woods vary widely in vessel diameter and density, with occurrences weighted toward the sparse-wide end of the scale; an inverse relationship between diameter and density is also evident.

Vessel Grouping and Nonrandom Vessel Arrangements

Most trees (~70%) have woods with vessels that are solitary and in radial multiples of two to four (IAWA Committee 1989; InsideWood 2004–). This is the default category in the IAWA coding system, as distinguished from woods with “vessels exclusively solitary (90% or more),” “radial multiples of 4 or more common,” or “clusters common” (IAWA Committee 1989, p. 242). Descriptions generally note the length of the radial multiples and sometimes the proportion of vessels that are solitary versus in pairs or longer radial multiples.

“Vessels exclusively solitary” occurs in a minority of woods (~10%–15% of diffuse-porous trees; InsideWood 2004–; Wheeler et al. 2007). In diffuse-porous woods, this feature is most prevalent in woods with narrow vessels (24% of taxa in the lowest vessel diameter category) and decreases with prevalence increasing vessel diameter but also occurs in some wide-vesseled woods (9% of woods with vessels >200 μm; InsideWood 2004–). It is generally considered the less derived condition and is found in 40%–45% of taxa in higher-latitude Cretaceous and early Paleogene fossil assemblages (Wheeler and Baas 2019). Solitary vessels usually occur with tracheids or vascular/vasicentric tracheids, elements that, if prevalent, can constitute a secondary conductive system (Carlquist 2013). This trait is also associated with axial parenchyma that is diffuse or diffuse-in-aggregates rather than elaborated paratracheal (InsideWood 2004–). High incidence in Australia is linked to the importance of families, particularly Myrtaceae, that typically show this feature (Wheeler et al. 2007). The association of solitary vessels and ring and semi-ring porosity is uncommon in trees but does occur, most notably in Fagaceae.

Vessel grouping (“radial multiples of four or more common” or “clusters common”) occurs at a frequency of ~10% in trees and is more common in the midlatitudes and in woods with narrower vessels (InsideWood 2004–). This character is rare or absent in Cretaceous woods (Wheeler and Baas 1991). Grouping may lessen vulnerability to cavitation and facilitate refilling of vessels (Baas and Carlquist 1985; Lens et al. 2011; Carlquist 2012, 2013). It can be important in dry regions, occurring, for example, in ~60% of trees in the dry Mediterranean to desert climates of Israel (Fahn et al. 1986). Occurrence is higher in dry and very dry tropical forests than in other tropical associations (Woodcock and Meyer 2020). Various ways of quantifying the degree of vessel grouping have been utilized (Carlquist 1984, 2013; Fahn et al. 1986; von Arx et al. 2013). Martínez-Cabrera and Cevallos-Ferriz (2008) found a significant relationship between the degree of grouping and the mean annual range of potential evaporation. Vessel clusters often occur with paratracheal (vasicentric to scanty) parenchyma, while radial multiples show a (less strong) association with apotracheal (diffuse to diffuse-in-aggregates) parenchyma (InsideWood 2004–). Vessel clusters and tangential clusters or bands often occur in ring-porous woods (InsideWood 2004–; Wheeler and Manchester 2007; Wheeler et al. 2007).

Vessels can also be arranged in diagonal, dendritic, or radial patterns or in tangential bands not necessarily involving contact between vessels. A tropical wood with diagonally arranged vessels (Calophyllum brasiliensis) is shown in figure 2B. Nonrandom vessel arrangements occur in <10% of trees (InsideWood 2004–). The anatomical diversity encompassed extends from the narrow, tightly clustered vessels in tangential bands in the latewood of some ring-porous trees (as in Ulmus) to the wide, solitary vessels in diagonal arrangements in diffuse-porous Fagaceae. In both of these examples, the woods also have subsidiary conductive elements (vascular/vasicentric tracheids): narrow and intermixed with the vessel clusters in Ulmus and irregularly shaped and adjacent to wide vessels in Fagaceae (IAWA Committee 1989; Wheeler and Manchester 2007).

Growth-Related Variation

Young trees typically produce wood varying in its characteristics from that produced later in growth. This juvenile period can last 5–20 yr (Panshin and Zeeuw 1970; Zobel and Sprague 2012). Conifers generally show the greatest differences between juvenile and mature wood (Panshin and Zeeuw 1970; Zobel and Sprague 2012), but hardwood trees typically show a marked increase in vessel diameter within the juvenile wood, as well as generally lower vessel density (Zobel and Sprague 2012). Transitions from diffuse-porous to semi-ring- and ring-porous have also been noted (Liu et al. 2020). There are indications of greater
genetic control over the characteristics of mature wood, suggesting that early growth may be more plastic and able to respond to environmental conditions (Lenz et al. 2010; Lachenbruch et al. 2011).

**Growth Rings**

Tree rings marking the cessation or slowing of growth are near universal in midlatitude trees and also occur in tropical trees. “Growth ring boundaries distinct” (IAWA Committee 1989, p. 234) occurs in 18%–22% of tropical South American trees in the InsideWood (2004–) database, although recent surveys generally indicate greater incidence (Silva et al. 2019; Marcelo-Peña et al. 2020). Growth rings are not necessarily produced annually, but even in the wet tropics tree species have been found that can be cross-dated and used in reconstructing yearly climate variability from tree cores (Holocene and Pleistocene climates; Granato-Souza et al. 2019). Although dendroclimatological parameters such as mean ring width and sensitivity have been used in interpreting fossil wood, Falcon-Lang (2005) discusses the problems inherent in attempting this type of analysis.

The IAWA coding system designates rings only as distinct or indistinct/absent on the basis of specified characteristics, with more detailed descriptions typically referencing the anatomical features delimiting the rings. Rings can be marked by variation in fiber thickness/dimensions, vessel diameter and density, frequency of parenchyma bands, marginal parenchyma, aspects of ray structure, or other features/combinations of features. Carlquist’s (2013) identification of 15 growth ring types illustrates the anatomical diversity associated with growth ring formation.

In the tropics, apart from the absence or rarity of ring porosity, rings show anatomical diversity similar to that seen in the midlatitudes. They occur at a moderate frequency across a range of vessel diameters and densities, even in woods with few wide vessels. With respect to the vessel-related features considered here, there is no clear pattern of occurrence, except for a weak relationship between growth rings and vessel density: an increase from 16% to 28% across the lowest to highest density categories in tropical South America (InsideWood 2004–). Occurrence of growth rings in the tropics is linked to seasonal variation in precipitation or flooding and, as in the midlatitudes, can involve production of multiple rings per year, but the response to climate is variable (Brienen et al. 2016; Silva et al. 2019).

**Vessels of Two Diameter Classes**

Some trees with diffuse-porous woods display a juxtaposition of wider and narrower vessels as observed in transverse section. This character is described in the IAWA coding system as “vessels of two distinct diameter classes, wood not ring-porous” (IAWA Committee 1989, p. 258) and, in trees, occurs only in the tropics (~2%–10% of tropical South American trees; InsideWood 2004–). Wood anatomists assess this character visually. Measuring 25–30 vessels at random as is typically done does not establish the presence of two diameter classes/populations of vessels; enlarging the sample size also cannot do this since random sampling tends to normalize distributions. More precise determinations require measurement of all the vessels within a given area, information presented in figure 5 for several Eocene fossil woods in the form of vessel diameter and position plots and diameter distributions. The diffuse-porous wood presented for comparison (fig. 5A) has vessels that are normally distributed. In contrast, the woods with interspersed wider and narrower vessels in figure 5B and 5C have diameter distributions that are significantly nonnormal and negatively skewed, with the suggestion of a smaller separate population of narrower vessels. In these cases, the presence of two populations cannot be established with certainty. This character tends to occur in certain families (both fossil woods are in the Anacardiaceae) and is often variably present. A check of the InsideWood database shows that, in woods of this sort, wider vessels generally predominate, but exceptions exist (Capparis maroniensis R.Ben, Uw 12107; InsideWood 2004–). These woods can be considered a functional equivalent of the ring- and semi-ring-porous woods of the midlatitudes.

It is common to find a range of vessel diameters in woody vines/lianas. The majority of lianas have this character present at least variably (InsideWood 2004–) and occurring with very wide vessels that are often densely arranged and associated with vasicentric/vascular tracheids, high/wide rays, and anomalous secondary growth (cambial variants/included phloem), a suite of characters recognized as typical of this life-form (Wheeler and Manchester 2002; Carlquist 2013). A fossil wood with many of these features (fig. 5D) has a broad, negatively skewed vessel distribution that is not clearly bimodal. Meunier et al. (2020), studying 14 liana morphospecies, found similarly broad vessel distributions tending to be negatively skewed. Some but not all of the distributions appeared to be bimodal, in agreement with results presented here and suggesting that designating vessel distributions as bimodal requires some caveats. These woods might be better described as appearing to have vessels in more than one diameter class (by analogy to InsideWood feature 89, “axial parenchyma in marginal or seemingly marginal bands”; IAWA Committee 1989, p. 276). Also of note is the occurrence in many lianas of vascular tracheids, narrow conduits (~20–35 μm) often intergrading with narrow vessels. Vasicentric tracheids are recorded in ~20% of lianas (InsideWood 2004–), showing that these taxa can have not only a range of vessel diameters but also a diversity in conduit types.

**Radial Variation in Vessel Diameter and Density**

Although many woods show some variability in vessel diameter along a radial axis, this variation is especially pronounced in the ring- and semi-ring-porous woods. The terms come from the wide and/or grouped earlywood vessels forming a ring that is often quite evident to the naked eye. In ring-porous woods, the earlywood vessels are considerably wider than the latewood vessels, and there is an abrupt transition across the ring. Semi-ring-porous encompasses woods in which (1) the transition to narrower vessels is more gradual or (2) there is a distinct ring of vessels along the growth boundary (IAWA Committee 1989). Gradations exist, and occurrence is to some degree facultative.

Ring and semi-ring porosity is known only in deciduous trees (Boura and De Franceschi 2007). This wood type is not represented among hardwood species in northern coniferous forests, undoubtedly because of the short growing season and susceptibility of wide vessels to freeze-related embolism. It is
Fig. 5  Eocene Piedra Chamana fossil woods. Shown are transverse sections, vessel diameter and position plots, and diameter distributions. A, Example of a diffuse-porous wood (*Luehea stratifica*ta Woodcock, Meyer et Prado). B, C, Woods with “vessels in two diameter [dia] classes” (cf. *Mangifera, Anacardium incahuasi* Woodcock, Meyer et Prado). D, Liana wood type (cf. *Thiloa*). Transverse sections are oriented horizontally to align with the diameter and position plots showing variation in vessel diameter along the radial axis. Boxplots show median, upper, and lower quartiles (ends of boxes) and the interquartile range (whiskers); the lower bracket shows the most dense 50% of data. Nonnormality was tested for using the Shapiro-Wilks (S-W) test. Modified from Woodcock and Meyer (2020).
common or predominant in midlatitude areas where the seasonal cycle is pronounced, temperatures fall below freezing, and water availability may be even more pronounced seasonally with the rise of the water table in the spring (Woodcock 1994). The near absence of ring and semi–ring porosity in the Southern Hemisphere has also been noted. The geologic record (Wheeler and Baas 2019) shows the rarity of ring and semi–ring porosity in the tropics and its increasing prevalence, with some variability, in the midlatitudes through the Cenozoic, likely associated with increased temperature seasonality/below-freezing conditions (Wheeler and Baas 2019).

A study of ring-/semi-ring-porous eastern North American trees (Woodcock 1989b) showed the occurrence of the vessel diameter distributions represented in figure 6 (which includes a diffuse-porous wood, Acer pensylvanicum; see fig. 6A for comparison). (1) Semi-ring-porous with a broad vessel diameter distribution that is negatively skewed (fig. 6B; Juglans cinerea). (2) Ring-porous with a broad diameter distribution that is positively skewed and probably bimodal, with a modal value in the narrow-diameter part of the distribution (fig. 6C; Carya tomentosa). (3) Ring-porous with a very broad diameter range (up to >350 μm) and two distinct and nonoverlapping populations of vessels (fig. 6D; Quercus macrocarpa). This species is in the white oak group (Quercus section Quercus; Hipp et al. 2020), which tends to have very narrow latewood vessels and a particularly sharp distinction between early- and latewood.

The potential utility of wood anatomical information in reconstructing annual climate variability has led to studies of the climate sensitivity of vessel diameter in trees. Most studies deal with ring-porous European Quercus, but some have been done on diffuse-porous species and semi-ring-porous Tectona L. (García-González et al. 2016; Buareal et al. 2020). Generally consistent findings are that earlywood vessel characteristics are decoupled from ring width and latewood features and are more plastic in their response to climate, show less pronounced growth trends, and respond to conditions during a relatively short period during or prior to growth initiation (Brienen et al. 2016). There is generally a positive relationship between earlywood vessel diameter/cross-sectional area and water availability, but negative relationships have also been noted (Woodcock 1989a; García-González and Souto-Herrero 2017). This research shows that the variation in vessel diameter especially evident in ring- and semi-ring-porous taxa allows for fine-tuning of the response to climate.

The occurrence of semi-ring-porous taxa in a lowland tropical forest assemblage from Peru dating from the Eocene and the rarity of this wood type in the present-day tropics occasioned a more detailed study of vessel patterning in the fossils (Woodcock and Meyer 2020). In this case, diameter and position plots aid in visualizing the patterning (fig. 7). All three woods show a gradual change in diameter across the ring and have significantly nonnormal diameter distributions. In the first example (fig. 7A; Dalbergia santa-rosa), the cross section and diameter and position plot show a gradual decrease in diameter across the ring, whereas the diameter distribution indicates the presence of two populations, a small population of wider vessels in the early part of the ring and a larger population of narrower latewood vessels. This pattern is similar, not to the semi-ring-porous wood, but rather to the ring-porous woods with bimodal diameter distributions shown in figure 6. In the second example (fig. 7B; Cordia asenjoi), there is a population of wider vessels in the first half of the ring, a more numerous population of medium-diameter vessels extending from the earlywood into the first part of the latewood, and a third population of very narrow vessels at

![Fig. 6](https://example.com/fig6.png)

**Fig. 6** Vessel arrangements and diameter distributions for ring- and semi-ring-porous North American woods, with a diffuse-porous species included for comparison. A, *Acer pensylvanicum* L. (diffuse-porous). B, *Juglans cinerea* L. (semi-ring-porous). C, *Carya tomentosa* (Lam.) Nutt. (ring-porous). D, *Quercus macrocarpa* Michx. (ring-porous). Modified from Woodcock (1989b).
the end of the ring. The third example (fig. 7C; *Lagerstroemia*) has a small population or outlier of wider vessels in the beginning of the ring and a larger population of narrow vessels occurring across the ring. In wood descriptions, the occurrence of two populations of vessels, while often assumed, is not often documented; the occurrence of three populations has not been previously described. The highly monsoonal climates of the Indian subcontinent are one place in the modern tropics where there are important forest trees with semi-ring-porous wood (*Tectona, Gmelina*, and species of *Lagerstroemia*). The Eocene fossil

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**Fig. 7**  Eocene Piedra Chamana fossil woods with semi-ring-porous wood. A, *Dalbergia santa-rosa* Woodcock, Meyer et Prado. B, *Cordia asenjoi* Woodcock, Meyer et Prado. C, Cf. *Lagerstroemia II* (Woodcock et al. 2017). Transverse sections are oriented horizontally to align with the diameter (dia) and position plots, showing variation in vessel diameter along the radial axis. Boxplots show median, upper, and lower quartiles (ends of boxes) and the interquartile range (whiskers); the lower bracket shows the most dense 50% of data. Nonnormality was tested for using the Shapiro-Wilks (S-W) test. RB = ring boundary. Modified from Woodcock and Meyer (2020).
woods occur at a paleolatitude of 13°S and may have been affected by the drier conditions found in the subtropics. Warm conditions in the late Eocene (Baatsen et al. 2016, 2020), linked to drier conditions and decreased water availability/high water stress, may also help to explain the semi-ring-porous component of this assemblage and the complex patterns these woods demonstrate.

These results can be summarized as follows. (1) Diameter and position plots considered together with cross sections and diameter distributions are helpful in representing and interpreting vessel patterning, especially when these are complex. (2) The distinction between ring- and semi-ring-porous woods may not be clear-cut when diameter distributions and spatial patterns are analyzed more closely. (3) Although semi-ring porosity is generally considered an intermediate condition between diffuse- and ring-porous, semi-ring-porous woods can have vessel distributions as complex as or more complex than those of ring-porous taxa. This point is illustrated here by the Peru fossils, but more detailed surveys at the drier margins of the tropics may identify similar wood types in the modern flora. (4) Studies of the climate sensitivity of vessels in ring-porous trees have advanced our understanding of the significance of variable vessel diameters.

A Typology of Vessel Patterning in Trees and Relationships to Climate

The typology presented in figure 8 is an attempt to summarize the diversity of vessel patterning in trees and show the range of variation in the character space found and associated ecological correlates. The extent to which the arrows indicate adaptive sequences is a separate question addressed below. Diffuse-porous woods with vessels that are solitary and in short radial multiples (central position) are taken as the starting point owing to the prevalence of these features and their simple vessel patterns. Tropical and midlatitude diffuse-porous woods are differentiated in terms of both the range of vessel diameters and densities represented and the values of vessel diameter and density that are most typical. The variation can be seen as falling into four main categories.

1. Growth-related variation (top left, black arrows). Included are (a) variation in vessel diameter and density in the transition from juvenile to mature wood seen generally in trees and (b) the growth rings that mark the cessation or slowing of growth in many trees (and all mid- to high-latitude trees) and can be expressed by aspects of vessel patterning (as in the ring/semi-ring-porous woods).

2. Woods with variable vessel diameter (top right and lower left, blue arrows). Here there is also a divergence between the tropics and midlatitudes: diffuse-porous woods with “vessels in two diameter classes” and woods with this characteristic plus wide, closely spaced vessels (liana wood type) occur in the tropics, while woods with radial variation (ring- and semi-ring-porous woods) are restricted almost entirely to the midlatitudes. (Semi-ring-porous woods include some tropical examples.)

3. Woods with grouped vessels (center right), including both long radial multiples and vessel clusters. These woods occur in both the tropics and the midlatitudes but are more prevalent in the midlatitudes; occurrence and degree of grouping are higher in drier areas.

4. Woods with nonrandom vessel arrangements (right side of diagram, orange arrows). Included are woods with vessels in radial, diagonal, or dendritic patterns or in tangential bands and also the ring- and semi-ring-porous woods. These types of arrangements put vessels in closer proximity than if they were arranged randomly and may occur with parenchyma or parenchyma bands and/or vascular/vasicentric tracheids. They also entail increased spatial differentiation of vascular-related features and those relating to support (the fiber fraction).

Differences between tropical and midlatitude woods can be looked at with reference to eastern North America, a region where temperature rather than precipitation is generally the important factor limiting ranges and geographical patterns are not overly complicated by topography. The vegetation of South Florida has ~90% of species that are exclusively tropical in their occurrence and at the northern limit of their distributions (Tomlinson 1980), including a diversity of palms. Trees are >70% broad-leaved evergreen and entire margined (Adams et al. 2008). Woods show types of vessel patterning (diffuse-porous woods with wide, sparsely occurring vessels and “vessels in two diameter classes”) and other features limited to or typical of tropical taxa (Woodcock and Meyer 2020). Northern range limits for these tropical taxa relate to some aspect of below-freezing temperatures but not simply frost occurrence (Sakai and Larcher 2012; Hoffmann et al. 2019). In the Asian tropics, the northern boundary of tropical vegetation is similarly distinct, although extratropical taxa and associations extend equatorward in the montane zone (Ashton 2014). Most of peninsular Florida north of South Florida supports subtropical evergreen vegetation (notophyllous broad-leaved evergreen vegetation forest of Wolfe [1979]) that is 40%–70% broad-leaved evergreen and entire margined (Adams et al. 2008) with woods that are diffuse-porous to semi-ring-porous. This vegetation type is not as extensive or diverse as in Asia (Ashton 2014), probably because of the susceptibility of eastern North America to incursions of polar air (Wolfe 1979). In northern Florida and to the north, deciduous forest associations have woods that are diffuse-porous, semi-ring-porous, and ring-porous and a significant component of diffuse-porous woods with scalariform perforations. The example from North America thus provides further evidence of the distinctness of the tropical flora in terms of wood anatomy.

The survey of fossil woods by Wheeler and Baas (2019) shows that differences between tropical and higher-latitude woods have persisted since angiosperms became forest dominants, including in periods such as the Cretaceous, when latitudinal temperature gradients were not pronounced. It also indicates that the tropical flora is typified by features considered more derived (simple vs. scalariform perforations, homocellular rather than heterocellular rays, etc.)—that is, it is more “modern” in its characteristics—compared with the higher-latitude flora, which shows time trends in many of these same character states.

The distinctness of the tropical flora clearly relates in part to factors limiting dispersal and radiation in the poleward direction—some aspect of below-freezing temperatures and possibly also subtropical aridity typical of the west coasts of continents. The range of climates existing in the tropics includes near-equatorial aseasonal climates in which supra-annual climate variability (El Niño/Southern Oscillation, etc.) is an important determinant of phenology; these climates are most extensive in
the Asian tropics and support highly diverse mixed dipterocarp rain forest (Ashton 2014). Away from the equator, there is a transition to climates with (a) two precipitation maxima or dry seasons and (b) one precipitation maximum in the high sun and a dry season of variable extent and severity. High temperatures coupled with variable precipitation create a wide range of climates in which moisture limitation is important. The highly monsoonal climates of the Indian subcontinent with semi-ring-porous dominants (*Tectona*) and the very dry climates with equable temperatures of coastal South America supporting *Prosopis*...
forests/woodlands or forests with pachycaulous trees (Ceiba, etc.) represent some of the extremes. Thus, the tropics present a rich template for the diversification of wood structures.

Adaptive Pathways

The typology is best thought of as representing broad convergences shaped by adaptation to the environment but also suggests possible adaptive pathways and evolutionary sequences occurring within clades. One example is the sequence from vessels that are solitary to vessels in short radial multiples to vessels in radial multiples of four or more (shown running from left to right in fig. 8). (The sequence from solitary vessels to clusters is not considered.) This would seem to be an easily achieved progression just requiring production of additional vessels in sequence by the vascular cambium. However, woods with solitary vessels often have tracheids—“fibres with distinctly bordered pits” in IAWA terminology (IAWA Committee 1989, p. 264)—rather than the “fibres with simple to minutely bordered pits” (IAWA Committee 1989, p. 264) that are more common in (angiosperm) trees (Carlquist 2013) and also diffuse axial parenchyma and heterocellular rays (InsideWood 2004–). All three features are considered less derived (Carlquist 2013; Wheeler and Baas 2019). Consequently, (1) tracheids may make up a secondary conductive system in woods with solitary vessels, obviating the need for vessel grouping, and (2) a transition from solitary to grouped vessels would likely require changes to a suite of characters integrated functionally and developmentally.

Furthermore, the middle character state in this sequence (diffuse-porous with vessels that are solitary and in short radial multiples) includes the woods with wide vessels that are prevalent in the tropics and often have elaborated paratracheal parenchyma. The end member in the sequence, “radial multiples of 4 or more common” (IAWA Committee 1989, p. 242), is, in contrast, most common in woods with narrow vessels and apotracheal parenchyma (diffuse to diffuse-in-aggregates or narrowly banded; InsideWood 2004–). The relatively few woods with wide vessels (100–200 µm) that are also grouped (many Sapotaceae) tend to have parenchyma of this type (InsideWood 2004–). Morris et al. (2018) document the relationship between vessel diameter and the presence/degree of axial parenchyma, interpreted as indicating the role of axial parenchyma fraction in xylem functioning. Consequently, (1) tropical woods with wide vessels and elaborated paratracheal parenchyma appear to constitute a distinct adaptive type, again involving integrated wood features, and (2) the transition to longer radial multiples may be more likely in narrow-vesseled woods.

Other examples could be considered, but the point is made that assessing the nature of specific adaptive pathways requires consideration of linkages between vessel-related characteristics and other aspects of anatomy. Vessel diameter, density, and patterning are not among the anatomical features included in the “major trends of xylem evolution” (quotations following Carlquist 2013) first studied by I. W. Bailey (Bailey and Tupper 1918). The latter include features relating to pitting and the presence and type (scalariform vs. simple) of perforation plates seen as making up a sequence accompanying shortening of the tracheary elements and fusiform cambial initials. The Baileyan trends can be considered unidirectional or at least not as easily reversible as features (like vessel diameter and density) less directly affected by the length of the cambial initials (Carlquist 2013). Thus, in the context of the typology, it is possible to recognize the anatomical diversification that has contributed to the success of angiosperm trees while still being subject to the necessary integration of wood anatomical features and the constraints this imposes on adaptive changes.

Discussion and Conclusions

This study provides a small demonstration of the anatomical diversity present in wood. A more complete idea can be had by consulting the list of variables included in the IAWA coding system (IAWA Committee 1989), representing only a fraction of the terms and features incorporated into the descriptions; considering that many taxa can be identified to the genus or species level on the basis of their wood; or reviewing virtually any publication on comparative wood anatomy by Sherwin Carlquist. New ways of representing vessel diameter and arrangement presented here further document this diversity. The multiplicity of features expressed in wood structure has important consequences for the development of fossil wood as a climate proxy. The first is that wood is itself a multiproxy source of information about climate and the environment. The second is that fossil wood assemblages with a diversity of taxa provide an array of indicators that can be analyzed in conjunction, checked for internal consistency, and used in paleoenvironmental reconstructions (Woodcock and Meyer 2020). Development of fossil plant proxies not reliant on taxonomic determinations is an important goal, but when fossil woods are also described and identified, floristic information can also then be used in conjunction with the anatomy-based analyses to support interpretations. Progress will rest on better information about geographic variation in wood characters and relationships to climate and the environment and a greater understanding of wood functional anatomy.

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Literature Cited

Adams J, W Green, Y Zhang 2008 Leaf margins and temperature in the North American flora: recalibrating the paleoclimatic thermometer. Glob Planet Change 60:523–534.
Ashton P 2014 On the forests of tropical Asia: lest the memory fade. Royal Botanical Gardens, Kew, UK.
Baas P, S Carlquist 1985 A comparison of the ecological wood anatomy of the floras of Southern California and Israel. IAWA J 6:349–353.
Baatsen M, DJ Van Hinsbergen, AS Von Der Heydt, HA Dijkstra, A Slijp, HA Abels, PK Bijl 2016 Reconstructing geographical
boundary conditions for palaeoclimatic modelling during the Ceno-
zoic. Clim Past 12:1635–1644.
Baatsen M, AS von der Heydt, M Huber, MA Kliphuis, PK Bijl, A Suijs, HA Dijkstra 2020 The middle to late Eocene greenhouse climate modelled using the CESM 1.0.5. Clim Past 16:2573–2597.
Bailey WW, WW Tupper 1918 Size variation in tracheary cells. I: A comparison between the secondary xylems of vascular cryptogams, gymnosperms and angiosperms. Proc Am Acad Arts Sci 54:149–204.
Boura A, D De Franceschi 2007 Is porous wood structure exclusive of deciduous trees? C R Palevol 6:385–391.
Brienen RJ, J Schöngart, PA Zuidema 2016 Tree rings in the tropics: insights into the ecology and climate sensitivity of tropical trees. Trop Tree Physiol 2016:439–461.
Brown HF, AJ Panshin 1940 Commercial timbers of the United States. McGraw-Hill, New York.
Buurle K, S Buajan, S Preechamart, C Muangsong, N Pumijumnong 2013 Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood. Springer, Berlin.
Carlquist S 1984 Vessel grouping in dicotyledon wood. Aliso 10:505–525.
——— 1998 Wood and bark anatomy of Caricaceae; correlations with systematics and habit. IAWA J 19:191–206.
——— 2012 How wood evolves: a new synthesis. Botany 90:901–940.
——— 2013 Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood. Springer, Berlin.
——— 2018 Living cells in wood. 3. Overview; functional anatomy of the parenchyma network. Bot Rev 84:242–294.
Carlquist S, DA Hoekman 1985 Ecological wood anatomy of the woody Southern Californian flora. IAWA J 6:319–347.
Chapoton SM, JH Razanamaharizaka, NM Holbrook 2006 A biomechanical perspective on the role of large stem volume and high water content in baobab trees (Adansonia spp.; Bombacaceae). Am J Bot 93:1251–1264.
Dyer JM 2006 Revisiting the deciduous forests of eastern North America. BioScience 56:341–352.
Elias TS 1980 The complete trees of North America: field guide and natural history. Van Nostrand Reinhold, New York.
Fahn A, E Werker, P Baas 1986 Wood anatomy and identification of trees and shrubs from Israel and adjacent regions. Israel Academy of Sciences and Humanities, Jerusalem.
Falcon-Lang HJ 2005 Global climate analysis of growth rings in woods, and its implications for deep-time paleoclimate studies. Palaeobiology 31:434–444.
Fern K 2018 Tropical plants database. http://tropical.theferns.info.
Fichtler E, M Worbes 2012 Wood anatomical variables in tropical trees and their relation to site conditions and individual tree morphology. IAWA J 33:119–140.
García-González I, M Souto-Herrero 2017 Earlywood vessel area of Quercus pyrenaica Willd. is a powerful indicator of soil water excess at growth resumption. Eur J For Res 136:329–344.
García-González I, M Souto-Herrero, F Campelo 2016 Ring-porosity and earlywood vessels: a review on extracting environmental information through time. IAWA J 37:295–314.
GBIF (Global Biodiversity Information Facility) 2020 The Global Biodiversity Information Facility. https://www.gbif.org/what-is-gbif.
Gorgens EB, AZ Motta, M Assis, MH Nunes, T Jackson, D Coomes, J Rossette, LEÖC Aragão, JP Ometto 2019 The giant trees of the Amazon Basin. Front Ecol Environ 17:373–374.
Granato-Souza D, DW Stahle, AC Barbosa, S Feng, MC Torbenson, G de Assis Pereira, J Schöngart, JP Barbosa, D Griffin 2019 Tree rings and rainfall in the equatorial Amazon. Clim Dyn 52:1857–1869.
Griggs MM 1990 Sassafras albidum (Nutt.) Nees. Pages 773–777 in RM Burns, BH Honkala, eds. Silvics of North America. Vol 2. USDA Forestry Service, Washington, DC.
Hacke UG, R Spicer, SG Schreiber, I Plavcová 2017 An ecophysiological and developmental perspective on variation in vessel diameter. Plant Cell Environ 40:831–845.
Hipp AL, PS Manos, M Hahn, M Avishai, C Bodénès, J Cavender-Bares, AA Crowl, M Deng, T Denk, S Fitz-Gibbon 2020 Genomic landscape of the global oak phylogeny. New Phytol 226:1198–1212.
Hoffmann WA, SW Flake, RC Abreu, NA Pilon, DR Rossatto, G Durigan 2019 Rare frost events reinforce tropical savanna–forest boundaries. J Ecol 107:468–477.
IAWA (International Association of Wood Anatomists) Committee 1989 IAWA list of microscopic features for hardwood identification. IAWA J 10:219–332.
InsideWood 2004– InsideWood database. http://insidewood.lib.ncsu.edu.
King DA, SJ Wright, JH Connell 2006 The contribution of interspecific variation in maximum tree height to tropical and temperate diversity. J Trop Ecol 22:11–24.
Lachenbruch B, JR Moore, R Evans 2011 Radial variation in wood structure and function in woody plants, and hypotheses for its occurrence. Pages 121–164 in FC Meinzer, B Lachenbruch, TE Dawson, eds. Size-and age-related changes in tree structure and function. Springer, Dordrecht.
Lens F, JS Sperry, MA Christman, B Choat, D Rabaey, S Jansen 2011 Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus Acer. New Phytol 190:709–723.
Lenz P, A Cloutier, J MacKay, J Beaulieu 2010 Genetic control of wood properties in Picea glauca—an analysis of trends with cambial age. Can J For Res 40:703–715.
Liu Y, L Zhou, Y Zhu, S Liu 2020 Anatomical features and its radial variations among different Catalpa bungei clones. Forests 11:824.
Marcelo-Peña JL, FA Roig, ZA Goodwin, M Tomazello-Filho 2020 Characterizing growth rings in the trees of Ñu: a wood anatomical overview for potential applications in dendroecological-related fields. Dendrochronologia 62:125728.
Martínez-Cabrera HI, SR Cevallos-Ferriz 2008 Palaeoecology of the Miocene El Cien Formation (Mexico) as determined from wood anatomical characters. Rev Palaeobot Palynol 150:154–167.
Martínez-Cabrera HI, E Estrada-Ruiz 2018 Influence of phylogenetic relatedness on palaeoclimatic estimation using angiosperm fossil woods. Ameghiniana 58:100.
Meunier F, SM Krishna Moorothy, H De Deurwaerder, R Kreus, J Van den Bulcke, R Lehebneh, H Verbeek 2020 Within-site variability of liana wood anatomical traits: a case study in Laussat, French Guiana. Forests 11:523.
Morris H, MA Gillingham, I Plavcová, SM Gleason, ME Olson, DA Coomes, E Fichtler, MM Klepsch, HI Martínez-Cabrera, DJ McGlinn 2018 Vessel diameter is related to amount and spatial arrangement of axial parenchyma in woody angiosperms. Plant Cell Environ 41:245–260.
Olson ME, T Anfodillo, JA Rosell, G Petit, A Crivellaro, S Isnard, C León-Gómez, LO Alvarado-Cárdenas, M Castorena 2014 Universal hydraulicities of the flowering plants: vessel diameter scales with stem length across angiosperm lineages, habits and climates. Ecol Lett 17:988–997.
Olson ME, JA Rosell, C Martínez-Pérez, C León-Gómez, A Fajardo, S Isnard, MA Cervantes-Alcayde, A Echeverria, VA Figueroa-Abundiz, A Segovia-Rivas 2020 Xylem vessel-diameter–shoot-length scaling: ecological significance of porosity types and other traits. Ecol Monogr 90:e01410.
Olson ME, D Soriano, JA Rosell, T Anfodillo, MJ Donoghue, EJ Edwards, C León-Gómez, T Dawson, JJC Martínez, M Castorena 2018 Plant height and hydraulic vulnerability to drought and cold. Proc Natl Acad Sci USA 115:7551–7556.

Panshin AJ, CD Zeeuw 1970 Textbook of wood technology: structure, identification, uses, and properties of the commercial woods of the United States and Canada. Vol 1. McGraw-Hill, New York.

Pfautsch S, M Harbusch, A Wesolowski, R Smith, C Macfarlane, MG Tjoelker, PB Reich, MA Adams 2016 Climate determines vascular traits in the ecologically diverse genus *Eucalyptus*. Ecol Lett 19:240–248.

Sakai A, W Larcher 2012 Frost survival of plants: responses and adaptation to freezing stress. Springer, Berlin.

Scipioni MC, RdP Salomão, AC Vibrams, HP Uller 2019 Decline in giant tree numbers: status report for Santa Catarina State and perspectives for Brazil. Florest Ambient 26:e20190039.

Silva MdS, LS Funch, LB da Silva 2019 The growth ring concept: seeking a broader and unambiguous approach covering tropical species. Biol Rev 94:1161–1178.

Stevens P 2001– Angiosperm phylogeny website. http://www.mobot.org /MOBOT/research/APweb/.

Tomlinson PB 1980 The biology of trees native to tropical Florida. Harvard University Printing Office, Cambridge, MA.

Venturas MD, JS Sperry, UG Hacke 2017 Plant xylem hydraulics: what we understand, current research, and future challenges. J Integr Plant Biol 59:356–389.

von Arx G, C Kueffer, P Fonti 2013 Quantifying plasticity in vessel grouping—added value from the image analysis tool ROXAS. IAWA J 34:433–445.

Wheeler EA 2011 InsideWood—a web resource for hardwood anatomy. IAWA J 32:199–211.

Wheeler EA, P Baas 1991 A survey of the fossil record for dicotyledonous wood and its significance for evolutionary and ecological wood anatomy. IAWA J 12:275–318.

——— 2019 Wood evolution: Baileyan trends and functional traits in the fossil record. IAWA J 40:488–529.

Wheeler EA, P Baas, S Rodgers 2007 Variations in dicot wood anatomy: a global analysis based on the InsideWood database. IAWA J 28:229–258.

Wheeler EA, SR Manchester 2002 Woods of the middle Eocene Nut Beds Flora, Clarno Formation, Oregon, USA. IAWA J 3(suppl):1–189.

——— 2007 Review of the wood anatomy of extant Ulmaceae as context for new reports of late Eocene *Ulmus* woods. Bull Geosci 82:329–342.

Wiemann MC, DL Dilcher, SR Manchester 2001 Estimation of mean annual temperature from leaf and wood physiognomy. For Sci 47:141–149.

Wolfe JA 1979 Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the Northern Hemisphere and Australasia. USGS Professional Paper 106. US Government Printing Office, Washington, DC.

Woodcock D 1989a Climate sensitivity of wood-anatomical features in a ring-porous oak (*Quercus macrocarpa*). Can J For Res 19:639–644.

——— 1989b Distribution of vessel diameter in ring-porous trees. Aliso 12:287–293.

——— 1994 Occurrence of woods with a gradation in vessel diameter across a ring. IAWA J 15:377–385.

Woodcock D, HW Meyer 2020 The Piedra Chamana fossil woods and leaves: a record of the vegetation and palaeoenvironment of the Neotropics during the late Middle Eocene. Ann Bot 125:1077–1089.

Woodcock D, HW Meyer, N Dunbar, W McIntosh, I Prado, G Morales 2009 Geologic and taphonomic context of El Bosque Petrificado Piedra Chamana (Cajamarca, Peru). Geol Soc Am Bull 121:1172–1178.

Woodcock D, HW Meyer, Y Prado 2017 The Piedra Chamana fossil woods (Eocene, Peru). IAWA J 38:313–365.

——— 2019 The Piedra Chamana fossil woods (Eocene, Peru). II. IAWA J 40:551–595.

Zobel BJ, JR Sprague 2012 Juvenile wood in forest trees. Springer, Berlin.