

On the possible functions of helical thickenings in conductive cells in wood

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Accepted for publication: 18 March 2023; published online: 31 March 2023

Summary – The career of Sherwin J. Carlquist was marked by numerous pioneering contributions to botany and especially to ecological and evolutionary wood anatomy. He developed some of the most important modern functional hypotheses for wood, including postulating a biomechanical and fluid dynamic role for helical thickenings (HT) in seasonally dry environments. Here we endeavor to honor Carlquist's legacy by summarizing existing observations, explicitly acknowledging that HT represent a range of non-homologous and likely functionally disparate features, and exploring HT functional hypotheses in light of data from a pantropical genus, *Croton*, in which HT are associated with mesic rather than xeric conditions. This is noteworthy in part because HT are commonly associated with the flora of temperate mesic areas and seasonally dry areas, particularly in non-tropical regions. Based on observations in *Croton*, the distribution of HT around the world, and interesting advances in fluid dynamics, we propose that diversity in this feature may serve two related functions in addition to the potential mechanical role previously articulated, namely, vessel refilling after cavitation and increased hydraulic efficiency.

Keywords – Sherwin Carlquist, helical thickenings, helical sculpture, secondary xylem, hydraulic architecture, refilling.

Introduction

Dr. Sherwin J. Carlquist made a number of seminal contributions to botany throughout his lifetime including important insights into island biology and the evolution of wood anatomy in ecological and functional contexts. He was arguably the most prolific wood anatomist in the history of the discipline, with a wide-ranging curiosity and incisiveness of observation and synthesis founded on the taxonomically widest breadth of studies of any worker. This breadth and depth of work has given rise to most of the critical hypotheses in wood evolution, many of which were recently reviewed (Olson 2020). Among of the abiding open questions in comparative, ecological, and evolutionary wood anatomy are the functions of helical thickenings (HT) in xylem, specifically in secondary xylem. To quote Carlquist (1980) "The effect of spirals, vested pits, and warty lumen surface on flow rates as demonstrated experimentally offers further opportunities, but integrating this with an interpretation that involves phyletic will evidently be one of the more difficult problems in wood anatomy." We endeavor here to honor Carlquist's legacy and attempt to address one portion of this challenge by briefly reviewing the history of HT in xylem with a special

emphasis on those thickenings found in conducting elements in secondary xylem. In so doing, we hope to synthesize existing observations and hypotheses to pose a framework to suggest further research into the function of HT in xylem.

HT NOMENCLATURE AND OTHER VESSEL-WALL SCULPTURE

Helical thickening (HT) is a term that has been used to encompass quite structurally and evolutionarily distinct (and thus homoplasious) anatomical features. Carlquist (1988) recognized this and introduced the concept of vessel wall sculpture to include all such features under one nomenclatural umbrella, though it is clear from his writings that there was no intent to suggest that all forms of helical wall sculpture are homologous, either evolutionarily or functionally. Specifically, vessel wall sculpturing includes HT, grooves interconnecting (confluent) pit apertures, and other vessel wall features that add a level of relief, such as verrucae, the warty layer, and vested pits.

HT are continuous layers of secondary wall deposition forming ridges on the lumen face of some plant cells' primary or secondary walls. Grooves interconnecting pit apertures, on the other hand, are depressions in the cell wall that resemble a helical pattern and may be mistaken for HT. The grooves may connect only two or three pit apertures of a vessel element or extend continuously across the intervessel face. Although grooves and thickenings are different phenomena, some species can have both: in *Clematis*, earlywood vessels have only grooves interconnecting pit apertures; in latewood, vessels have grooves with thickenings on either side of the grooves. Occasionally, other wall sculptures, such as reticulate thickenings in *Juglans*, are found, but they do not display a helical pattern (Carlquist 1988).

Several other terms can be found in the literature, including "spiral thickenings" (Metcalf & Chalk 1950; Panshin & de Zeeuw 1970; Parham & Kaustinen 1973; Ohtani & Ishida 1978), "tertiary helical thickenings" or "tertiary spiral thickenings" (Hiley 1919; Church 1920; Frost 1931; Sax & Abbe 1932; Bierhost & Zamora 1965), and "helical bands" (Itoh 1974). Carlquist (1988) rejected these terms, pointing out that "spiral" is a two-dimensional structure in geometry while a helix is three-dimensional, thus more appropriate. Historically, the term "tertiary helical thickenings" (discussed in Ohtani & Ishida 1978), was used because it was believed that these thickenings comprised a wall layer in addition to the secondary wall and "helical bands" is a term that Carlquist reserved for the secondary wall pattern of the primary xylem. In this paper, we adopt "helical thickenings" (HT) for both hardwoods and softwoods as a matter of convenience, and because we are not addressing grooves interconnecting pit apertures, verrucae, vestures, or the warty layer.

THE DISTRIBUTION OF HT IN PLANT GROUPS AND ORGANS

The distribution of HT varies among different plant groups and organs, as they can be found in ferns (Pande 1935; Leroux *et al.* 2011; Hernández *et al.* 2013), gymnosperms, and angiosperms (Record 1919), occurring in various parts of the plant, including leaves (Gray 2014), flowers (Woodson & Moore 1938; Boyle 1980; Abdelhafez *et al.* 2020), fruits (Tukey & Young 1942; Gañán *et al.* 2008), seeds (Rodin & Kapil 1969), roots (Gasson 1979) and stems. While a single term is usually used to refer to HT, given the phylogenetic breadth of the groups over which HT are found, they are clearly homoplasious features of xylem (Carlquist 2012), whether primary (found in all vascular plants) or secondary (restricted to but not ubiquitous in seed plants).

Primary xylem originates from the procambium of apical meristems during primary growth and consists of protoxylem and metaxylem. Protoxylem is the first to develop, formed before or as an organ is elongating, and is characterized by small-diameter conducting elements with typically unlignified primary walls and lignified annular and/or helical secondary thickenings. Metaxylem conducting elements may have helical, annular, scalariform, and/or reticulate thickenings and may or may not have pitted, lignified secondary walls. These thickenings of primary xylem conducting elements are assumed to provide mechanical support to prevent collapse in xylem in primary tissues,

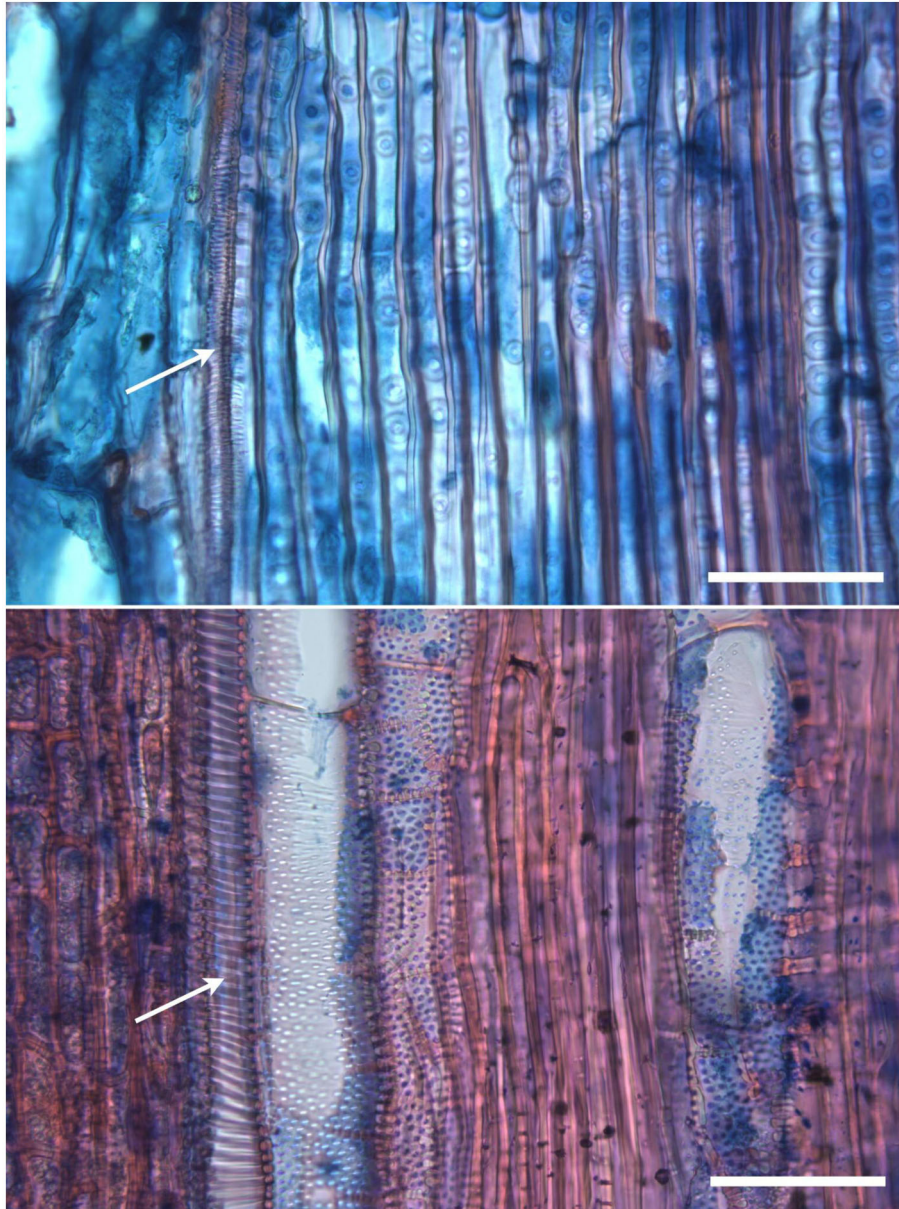


Fig. 1. Radial sections showing helical thickenings (arrows) in the primary xylem of *Pinus strobus* (top) and *Fraxinus pennsylvanicum* (bottom). The conducting elements in the adjacent secondary xylem lack helical thickenings in both species. Scale bars = 60 μm.

many of which are required to have mechanical flexibility while subject to high internal negative pressures (Record 1919; Esau 1960) (Fig. 1), and further have been shown to influence capillary flow rates (Jeje & Zimmerman 1979).

Considering that this manuscript deals with the potential functions of HT in conductive cells in wood, we will restrict the balance of our review to HT in the secondary xylem unless otherwise stated. Secondary xylem elements originate from the vascular cambium, and a lignified secondary wall is in most cases formed after cell elongation.

Within the secondary xylem in angiosperms, HT can be found in vessels (throughout the body or only in their tails), vascular/vasicentric tracheids, and ground tissue fibers, but very rarely in axial parenchyma (IAWA Committee 1989). In ring-porous woods they are more pronounced in latewood vessels than in earlywood vessels (Carlquist 1975, 1982b), possibly suggesting a correlation with xeromorphy (Calquist & Hoekman 1985, though see below for other interpretations). When present in diffuse-porous woods with a non-uniform distribution of HT, they are more pronounced in narrower vessels. Vasicentric tracheids may also exhibit HT and, in general, they appear similar to those of the vessels with which they are associated (Carlquist 1988). In ground tissue fibers (*sensu lato*) and axial parenchyma, HT is rare, which according to Carlquist (1988) is to be expected since these types of cells are essentially non-conductive. Fibers with distinctly bordered pits are more likely to exhibit HT than fibers with simple to minutely bordered pits; however, HT only occur in fibers if they are also present in vessels of the same wood.

In gymnosperms, axial tracheids can exhibit HT, usually extending over the entire cell body. They may be well developed throughout the growth increment, while in other cases, they may become more prominent only in earlywood or latewood (Panshin & de Zeeuw 1970, IAWA Committee 2004), and in some taxa can be found in ray tracheids (IAWA Committee 2004).

HELICAL THICKENING CLASSIFICATION

By studying the variations in types of HT, authors have classified them as S or Z based on the orientation of the helices when evaluated from outside the cell. The thickenings may consist of one helix or a series of parallel helices arranged in a branched or unbranched manner around the lumen of the cell. Some woods exhibit only one type of HT, while others may display several types, the typology of which is briefly reviewed below.

Parham & Kaustinen (1973) investigated the variability of helical thickening in three softwoods and nineteen hardwoods. They described the branching patterns, the spacing between helices, and the nature of their attachment to the cell wall. In their study, HT were classified into three major categories — unbranched or seldom so, branched, and swirled — which were further subdivided into Type 1 — helices closely bound to the lumen surface and occasionally merging with it. Type 2A — very prominent helices, somewhat or very loosely attached to the cell wall; type 2B — very prominent helices firmly attached to the cell wall; and Type 2C — a combination of types 2A and 2B.

Meylan & Butterfield (1978) noted the limitations of Parham & Kaustinen's (1973) classification, which relied on a limited number of species. They proposed a new classification based on a survey of the anatomy of 178 species of New Zealand native woods. The following four categories of HT were described: (i) fine striations; (ii) light HT sometimes merging with the vessel wall; (iii) prominent HT; and (iv) very close prominent HT. They acknowledged that it may sometimes be challenging to place the HT of wood into a particular category and that some species have more than one type of thickening, varying between earlywood and latewood.

Ohtani & Ishida (1978) described in detail many forms of HT to improve the identification of 218 hardwood species from Japan, classifying them into four major types according to the helical direction within a vessel member. Types 1 and 2 are referred to as S-direction and Z-direction HT, respectively, which can be further subdivided into branched and unbranched. Type 3 is characterized by a combination of S and Z spiral thickenings, while type 4 is characterized by localized thickenings without helical arrangement.

To simplify and standardize the description of HT for wood identification in softwoods, an IAWA committee (IAWA Committee 2004) established a set of HT-related characters. In defining the character states, they discuss the grouping, spacing, inclination angle, thickness, branching, and degree of attachment of HT to the inner cell wall (IAWA Committee 2004), though not all these parameters appear in the character-space. They note that the spacing of the HT may be correlated with both the inclination angle and thickness, with narrowly spaced HT being thinner and forming a larger angle with the cell axis compared with widely spaced HT (IAWA Committee 2004), a detail to which we will make reference later in this manuscript.

Despite these efforts to characterize and establish a taxonomy for HT, none of the above-noted schema are widely adopted. This may in part be a result of the anatomical variability of HT that each of the publications clearly note, and also a result of the phylogenetic breadth across which they are found. A “failure” to have a standard nomenclature may in fact merely be symptomatic of the fact that HT as a term is a broad category in which anatomically (and perhaps functionally) disparate cell features are artificially grouped. To understand how this came about, and how it may be a desirable outcome, it is illuminating to briefly examine when and how HT in wood have been observed and interpreted.

HISTORICAL REPORTS OF HT IN WOOD

HT were among the earliest reported features in plant anatomy. Despite the archaic instruments available in the seventeenth century, HT were illustrated in the works of Malpighi (1628–1694), Grew (1641–1712), and van Leeuwenhoek (1632–1723), as cited in Baas (1982). While these authors incorrectly attributed vessel function to air transport based on a comparison of HT with insect tracheae and mammalian bronchiae, Hooke’s suggestion in 1665 (as cited in Baas 1982) that plants contain “natural and innate juices” within their vessels provided an early critical observation that would later establish xylem as a water conducting tissue.

As noted by Baas (1982), the eighteenth century contributed comparatively little to the advancement of wood anatomy, but in the nineteenth century wood anatomy began to flourish. Link (1839–1842), as cited in Bierhorst & Zamora (1965), identified “spiral elements” and a variety of other types of tracheary elements, which he named “spiroids”. Hugo von Mohl (1851) observed plant growth and development and, in the context of primary xylem, concluded that in vessels that mature after organ elongation HT appear close together. However, if the organ undergoes elongation while or after the vessel develops, the HT are drawn apart, making them appear loose.

With the development of systematic wood anatomy in the following decades, a more explicitly evolutionary view of HT (and wood anatomy in general) matured, with multiple studies documenting the presence of HT in woods across a wide taxonomic and geographic range. Sanio (1863) observed the presence of HT in vessel elements of *Myrtus communis* (cited in Schmid & Baas 1984) while Moll & Janssonius (1908) documented their presence in the woods of Java. Record (1919) published the first comprehensive phenomenological report listing the families and genera in North America containing HT and corroborating the concept that the presence of HT is a useful diagnostic feature for wood identification, as well as discussing the considerable variation in morphology and distribution within the plant, and correlated the presence of HT with other characteristics, such as their presence in vessels with smaller lumina. Kanehira (1921) reported the presence of HT in *Gleditsia* and *Elaeocarpus* and as a result of his research he addressed the concept of HT related to climate. Frost (1931), influenced by Bailey & Tupper’s (1918, 1919) ideas regarding phylogenetic wood anatomy and major trends in structural specialization of anatomical elements, observed that HT most commonly occur in woods with simple perforation plates. One result of these more floristic-like surveys (even if in the context of providing characters for wood identification) was the growing awareness of the correlations between HT and plant ecology in a broad sense.

HT in ecological (comparative) wood anatomy

Ecological and comparative wood anatomy studies have also contributed to our understanding of HT occurrences because these approaches help us infer how natural selection shapes wood anatomy in the context of habit and habitat. Several pre-Carlquist comparative wood anatomical works mention HT, including Tippon (1938) in Moraceae, Moseley (1948) in Casuarinaceae, Stern (1954) in Lauraceae, Canright (1955) in Magnoliaceae, and Mosely & Beeks (1955) in Garryaceae. An important source of information regarding HT is the study of geographically disparate floras that report this feature and correlate it with ecological distributions, including Moll & Janssonius (1906–1936), Kanehira (1921), Weber (1936), Metcalfe & Chalk (1950), Patel (1967, 1973, 1974), Meylan & Butterfield (1978), Baas &

Carlquist (1985), Carlquist & Hoekman (1985), Fahn *et al.* (1986), Zhang & Baas (1992) and Rosell *et al.* (2007). Several authors observed that the distribution of species with well-developed HT appears to be associated with two main environments: seasonally dry areas, particularly at non-tropical latitudes, and temperate mesic areas (Wheeler & Baas 1993).

Moll & Janssonius (1908) may have been the first authors to note that HT occur more often in temperate species than tropical ones when they observed the lower frequency of this feature in Java's flora. This is consistent with the findings of Kanehira (1921), who concluded that the presence of "spiral markings" appears to be influenced by climatic conditions (as related to latitude), finding that a small percentage of tropical woods and a high percentage of temperate woods possess HT. Record (1934, 1943) indicated that HT were much less common in tropical woods than in those of the temperate zone, and in a study of desert shrubs Weber (1936) revealed HT to be extremely common. Metcalfe & Chalk (1950) reported the presence of HT in fibers and vessels of several hardwood families.

Carlquist (1957, 1959) suggested that different types of vessel wall sculpture could have emerged independently, under different circumstances, in different groups, which is a position that we support and is in keeping with earlier hypotheses (Wiedenhoef 2008, unpublished thesis). This is also consistent with the fact that various types of HT (Kanehira 1921, Parham & Kaustinen 1973, Meyland & Butterfield 1978, Ohtani & Ishida 1978) have clearly evolved multiple times in a systematically diverse set of woods.

Most tropical taxa do not exhibit HT, except for families such as Rosaceae, Aceraceae (Sapindaceae), and Ericaceae (Wheeler & Baas 1993), and most of these lineages come from northern temperate regions. In Fabaceae, found in most of the vegetation types in the world, HT are generally absent in tropical taxa, but are observed mostly in latewood vessels of ring-porous taxa and/or taxa from seasonally dry habitats (e.g., *Gleditsia*, *Sophora*, *Robinia*, *Gymnocladus*, *Cladrastis*, *Laburnum*, *Maackia*, *Cytisus*, *Lotus*, *Ulex*). Figure 2 shows the prevalence of HT and ring porosity in hardwoods, and HT in softwoods worldwide as represented by percentages of records in the InsideWood database (InsideWood 2004-onwards). For hardwoods our searches were limited to taxa containing vessels, resulting in 7696 records, of which 2135 were temperate and 5561 were tropical. In the case of softwoods, the database contains 235 records, of which 185 are temperate and 50 are tropical. We recognize a strong temperate bias in collections, historical and current funding for scientific research, published literature (Slik *et al.* 2015), and the available descriptions in InsideWood, so these metrics are presumed to overrepresent the relative abundance of temperate-correlated characters and are intended to be illustrative rather than definitive.

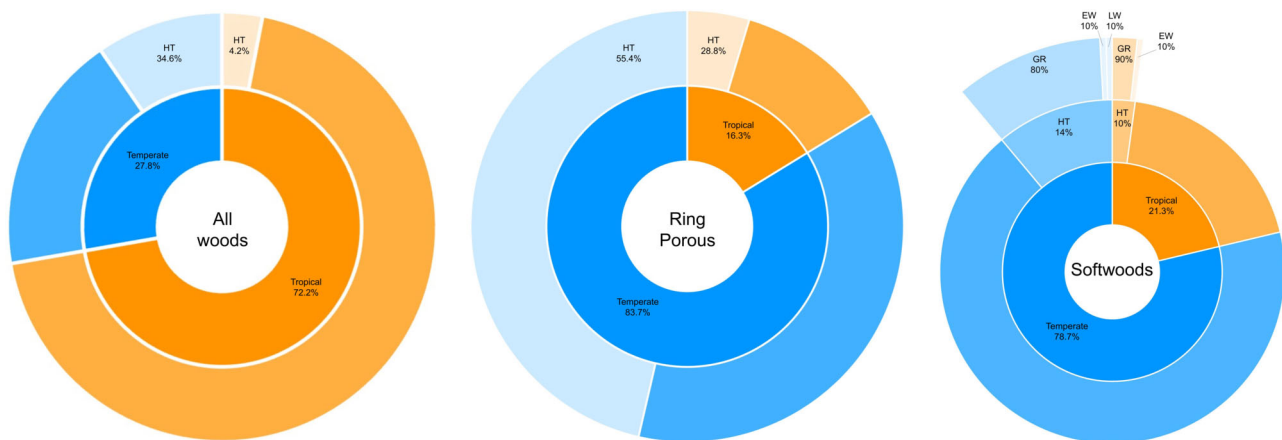


Fig. 2. Summary data from the InsideWood database showing the prevalence of helical thickenings (H.T.) in temperate and tropical species worldwide (left), the prevalence of helical thickenings (H.T.) in ring-porous species in temperate and tropical areas (center), and the distribution of HT in softwoods (right). See section Survey data of wood anatomical patterns for more information.

Softwoods are typically distributed in temperate climates (78.7% of all softwoods in InsideWood are temperate), but the percentage of HT in temperate softwoods (14%) is lower than that in temperate hardwoods (55.4%). Moreover, we can observe that in softwoods helical thickenings are more commonly found throughout a growth ring (80%–90%) as opposed to only occurring in earlywood or latewood.

In hardwoods, ring porosity is a predominantly temperate phenomenon (83.7% of all ring-porous woods are temperate) and is also often associated (55.4%) with HT. Approximately 28% of all woods in InsideWood are temperate, and 34.6% of all temperate woods have HT. In contrast, only 4.2% of tropical woods possess HT, although there is likely to be a degree of underreporting, since research biases can influence how carefully researchers search for characters that they do not expect to be present. These data are comparable to percentages published by Wheeler & Baas (1993) that focus on the relation between climate and wood anatomy, partially because the InsideWood data are derived to some degree from the Wheeler and Baas data set. However, we emphasize again that the percentage of temperate wood species in the InsideWood database may be overrepresented since some geographic regions, primarily tropical, need to be further explored (Cazzolla Gatti *et al.* 2022). Current estimates of tropical tree species range from 37 000 to 53 000 (Slik *et al.* 2015, Beech *et al.* 2017) contrasting to approximately 5561 tropical species represented in InsideWood, or the 124 species of woody plants in temperate Europe (Slik *et al.* 2015).

Regardless of which authors were addressing the prevalence and distribution of HT, one core question remained open — what are the functions of HT? As we noted above, a plausible mechanical understanding of the role of annular and HT in primary xylem has been fairly well-developed for centuries, and more recent work on the role of HT in improving flow rate in primary xylem is suggestive. We are of the opinion, given the breadth of HT structure, the disparate environments in which they occur, and the many lineages that produce them, it is improbable that there is a single, overarching mechanistic explanation for their function(s) in wood.

Functional hypotheses for HT in wood, and a case-study in *Croton* (Euphorbiaceae), a predominantly xeric tropical lineage with mesic associations for HT

There are three primary hypotheses for the function of HT in conducting elements in wood, each of which will be addressed in subsequent sections: (1) mechanical strength to resist implosion forces related to high xylem tensions, typically in the context of xeric taxa; (2) lumen wall wettability, whether in the context of adhesion of water molecules to the lumen wall to resist cavitation or conduit refilling; and (3) possible increase in conductivity/reduction in flow resistance. It is essential to reiterate that HT encompass a variety of sometimes disparate helically arranged thickenings in a wide range of taxa, and we consider it almost certain that the function of HT vary from taxon to taxon according to the physiological and environmental conditions of that plant — that is, we consider it improbable that there is one function of HT in wood. To elucidate our positions with regard to these hypotheses, we introduce data from *Croton* (Euphorbiaceae), a pantropical genus with a well understood phylogeny (Berry *et al.* 2005a,b, 2007, Arévalo *et al.* 2017) and a comparatively well-developed corpus of wood anatomical data (Wiedenhoeft 2008, unpublished thesis; Arévalo *et al.* 2017), wherein HT in vessel elements have evolved multiple times, and are unambiguously associated with mesic and not xeric habitats (Arévalo *et al.* 2017).

FUNCTION 1: PREVENTING CONDUIT COLLAPSE (MECHANICAL HYPOTHESIS)

One of the first functional hypotheses for HT related to mechanical strength was proposed by Carlquist (1975). He wanted to provide a functional explanation for the observed correlation between HT and latitude and their presence in desert woods. Although there were no experimental studies to support his hypothesis, he suggested a reasonable explanation: HT on the walls of xylem vessels appeared to offer mechanical strength to resist vessel implosion, preventing collapse under conditions of high negative pressure. He also proposed that HT enhance flexibility in woods subjected to conditions of high wind thrust. Similarly, Carlquist (1992) described a band-like thickening on

vessel walls of Cucurbitaceae, suggesting an increase in wall strength to compensate for the large diameter of the vessels in woody vines.

Some authors argue that HT do not contribute to the mechanical strength of vessels in wood (De Micco *et al.* 2008). Baas (1986) argues that wood is a cohesive tissue, with vessels and surrounding cells that are flexible, therefore, negative pressures cannot damage individual cells, despite the high tensions. He also mentioned that vessel collapse has never been documented in wood anatomical studies.

Hacke *et al.* (2001) reject Baas's idea, proposing that implosion could occur sporadically due to a damaged wall incapable of sustaining the pressure difference between gas- and water-filled conduits that had not already caused air entry at the pits, but note that even in this scenario, the initial rupture of the wall would cause immediate air-seeding and prevent implosion. Actual vessel collapse could only occur if the wall were then so fragile that it collapsed under the at-most-slightly negative post-cavitation pressure. Sperry (2003) notes that tracheary collapse is rare, indicating that cavitation occurs before implosion pressures are reached. He estimates that a "minimum safety factor for implosion (implosion/cavitation pressure) ranges from 1.7 in angiosperm vessels to 6.8 in conifer tracheids".

There is thus some debate about whether xylem tension can cause the conduits in wood to implode or collapse, but depending on the conduit structure, the plant organ, and biomechanics, partial collapse could be reversible (Cochard *et al.* 2004, Brodribb & Holbrook 2005). It has been suggested that the mechanical strength of surrounding tissues is vital to prevent vessels from collapsing (Jacobsen *et al.* 2005, 2007). However, there remains no direct evidence that HT prevent the collapse of conduits in wood.

FUNCTION 2: LUMEN WALL WETTABILITY HYPOTHESIS

Carlquist (1980, 1982a) expressed concern over the lack of explanation for the function of HT in dicotyledon vessels. In his opinion, the hypothesis proposed by Jeje & Zimmermann (1979) — that helices can increase water flow — would not be the selective factor that resulted in the evolution of this feature in wood. Therefore, he hypothesized that the increased surface area offered by HT and other forms of wall relief would facilitate hydration — the bonding of water molecules to surfaces, later referred to as wettability. He explained that an increase in wettability within a vessel element or tracheid could facilitate the tolerance of a higher water column tension within the vessel or tracheid without rupture which would result in fewer cavitations, though we are not aware of any data to show that this is the case.

Inspired by reports that roughness enhances wettability, Kohonen (2006) investigated the hypothesis that wall sculpturing increases wettability in *Callitris*, demonstrating that roughness can dramatically decrease the contact angle of water with the tracheid lumen walls. Moreover, he speculated that HT could also result in enhanced wettability. Kohonen & Helland (2009) demonstrated that HT reduced the contact angle between water and vessel walls, resulting in enhanced wall wettability.

It is important to note that most concepts of embolism in wood involve air-seeding from an adjacent air-filled cell (Zimmerman 1983), or spontaneous nucleation of cavitation as a result of high xylem tensions (Pickard 1981; Zimmerman 1983) and the presence of dissolved gases in the transpiration water (see Lens *et al.* 2022 for a thorough discussion of these and others). For the former case, it is not entirely clear how lumen wall wettability/hydration would inhibit cavitation, as once air enters it will expand as a result of the negative pressure — enhanced hydrogen bonding of the water to the lumen wall should not prevent the spread of such an embolism. In the latter case, wettability and contact angle are only measurable/relevant in the context of an air-water interface — in a filled conduit there is no such issue. It is not clear how surface roughness or HT would increase resistance to cavitation, whereas it is clearly shown to improve wettability in the presence of an air-water interface, such as in the case of conduit refilling.

FUNCTION 3: INCREASE IN CONDUCTIVITY/REDUCTION IN FLOW RESISTANCE HYPOTHESIS

Plant water flow studies are challenging because of the small size of xylem conduits and complex internal flow phenomena (Tyree & Zimmermann 2002) and they have been primarily the purview of plant physiological experiments (Zimmermann 1983). Jeje & Zimmermann (1979) investigated the relationship between HT and flow resistance in vessels of the primary xylem, concluding that vessels with wall sculpturing had higher flow rates in instances of capillary flow refilling air-filled vessels at ambient pressure. Carlquist (2012) rejected Jeje & Zimmermann's (1979) idea that HT accelerate flow since helical sculpturing is more common in plants of colder or drier habitats, and is more pronounced in latewood than in earlywood, making it more prominent in vessels where flow is typically slower. As will be explained in greater detail later, we suggest that smaller conduits with otherwise reduced flow rates are exactly those in which greater flow/reduced resistance would be most beneficial to the plant.

A theoretical fluid dynamic analysis by Wang (2006) demonstrated that, for cases with low Reynolds numbers, conduits with helical corrugations can exhibit optimal relationships between corrugation size, angle, and spacing to maximize rotational flow by reducing lumen wall resistance to flow. This is also consistent with large scale flow of water in civil engineering, where flow can be improved by helical or corrugated tubing, though the boundary conditions of the continuous column of water under tension *in planta* and bulk flow through tubes containing air-water interface under positive pressure or gravity are not directly intercomparable. Thus, if Wang (2006) is correct, HT in xylem conduits could induce resistance-lowering rotational flow and thereby increase overall flow, especially in narrow conduits where both total fluid volume and maximum distance from the lumen wall is small.

CASE STUDY IN *CROTON* (EUPHORBIACEAE)

To contextualize these three hypotheses, we recapitulate some of the results of Wiedenhoef (2008) and Arévalo *et al.* (2017) on the evolution of wood anatomical diversity in the context of phylogeny, habit, and habitat in *Croton* (Euphorbiaceae). Extant *Croton* are largely xeric, with an inferred mesic progenitor, and comparatively frequent HT in the vessel elements for a predominantly tropical taxon. The vessels of most *Croton* species lack HT, but most of those that have them bear them only in their tails (Fig. 3) (Wiedenhoef 2008; Arévalo *et al.* 2017). Four species, one (*Croton alabamensis* (Fig. 4A, B)) from one of the two major subgenera of the genus, and three species (*C. fruticosus* (Fig. 5C, D), *C. lanatus* (Fig. 5C, D) and *C. flavispicatus* (Fig. 5A, B)) from the other, are the only known *Croton* that bear distinct HT throughout the body of the vessel elements.

C. fruticosus shows neither geographic nor elevational variation in the presence or abundance of HT in the vessel elements, based on a review of specimens taken from twelve herbarium sheets. HT were present in all specimens from Texas (10 specimens, each from a different locale), Arizona (1 specimen), and New Mexico (1 specimen). Furthermore, greenhouse-grown *C. alabamensis* also showed HT typical of wild-grown material. This suggests that the development of HT in this species — found across geographic, elevational, and climatic gradients, including the greenhouse — is either constitutively expressed, or whatever stimuli necessary to induce their formation are present in all these instances. No additional specimens of *C. lanatus* or *C. flavispicatus* were available to determine if helical thickenings are found across the range of these taxa. *Croton fruticosus* is one of the northernmost *Croton* and grows in xeric environments in Mexico and the American southwest — similar to the findings of Weber (1936) or Carlquist & Hoekman (1985), but interestingly, closely related congeneric species with similar geographic range lack HT. *Croton alabamensis*, another of the northernmost *Croton*, is not closely related to *C. fruticosus*, and grows in comparatively mesic conditions in Alabama and Texas. With the exception of the four *Croton* species mentioned above, all other species in the genus with HT bear them only in the tails and not throughout the body of the vessel elements.

Carlquist & Hoekman (1985) postulated a function for HT in vessels related to cavitation and vessel-collapse resistance in seasonally dry, Mediterranean-type environments. We believe that the latter hypothesis is not the most plausible for *Croton* (and probably not for other woods as well) for several reasons: first, for a vessel to collapse from xylem tension, the tension of the xylem sap would have to be sufficient to generate implosion force. While pure

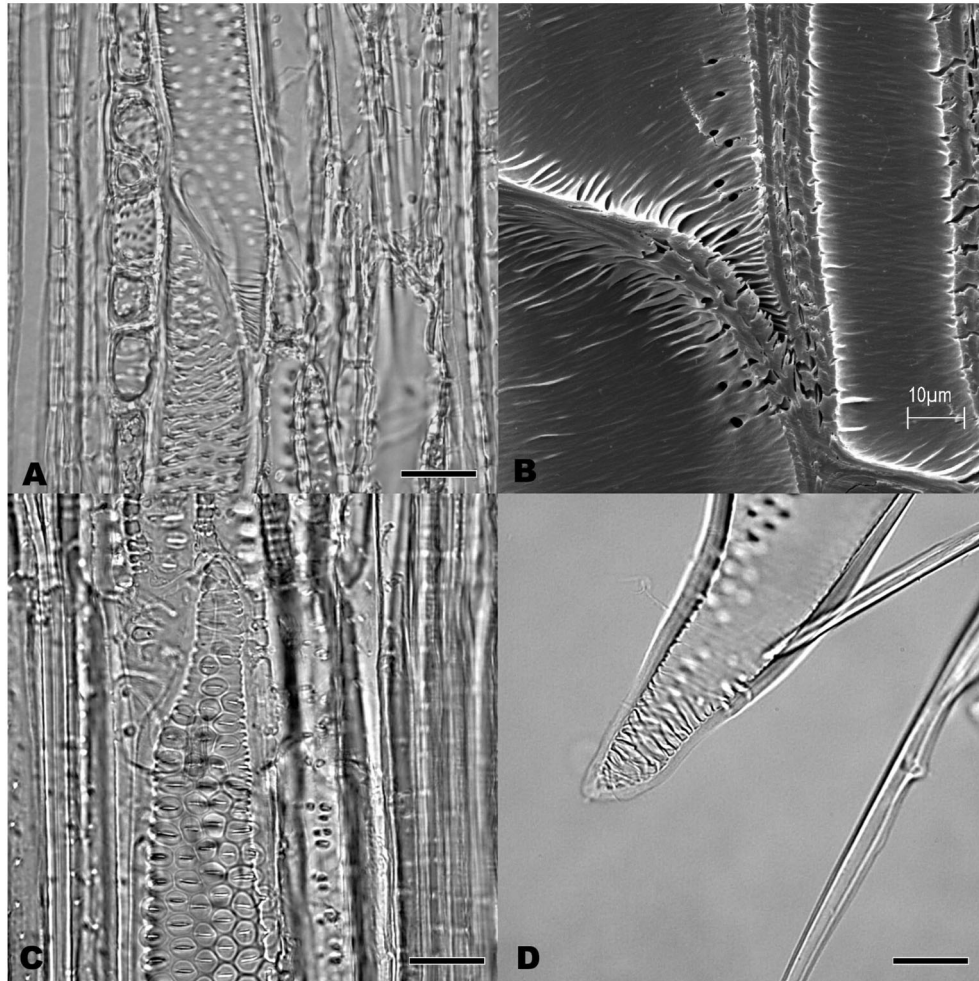


Fig. 3. Light and scanning electron micrographs showing helical thickenings restricted to vessel element tails. (A,B) *Croton maestrensis* (HAJB 81958); (C) *Croton nubigenus* (van Ee 587); (D) *Croton poecilanthus* (van Ee533). Scale bars: A, C, D = 20 µm. In the case of *C. maestrensis*, the helical thickenings continue a short distance into the body of the vessel element; there is a faint continuance of helical thickenings into the body of a vessel element from *C. poecilanthus*, shown in D, as well.

water can sustain higher tensions, there is no evidence that the hydrogen bonding of the transpiration sap (which is not pure water, and thus can sustain lower tensions) to the lumen face of the cell wall (necessary to transmit the implosion force) is of sufficient magnitude. Second, vessel elements are not hollow tubes unsupported in a system at atmospheric pressure (as with a straw analogy, Brodribb & Holbrook 2005). Instead, they are fixed in a matrix of other cells, each of which are adhered to each other by lignin in the compound middle lamella (Baas 1986, De Micco *et al.* 2008). This means that a vessel implosion force would have to first overcome the adhesive-like bonds between a vessel and its adjacent cells. As noted above, we know of no reported cases in the literature of mature vessels in wild-type wood showing signs of collapse due to implosion caused by xylem sap tension in any environment. A third point arguing against this interpretation is less concrete and speaks to the initial predicate for the hypothesis, rather than evidence to support or refute it; we suggest that the external stimulus driving the presence of HT in conduits may not be seasonal dryness, per se, but rather seasonal wetness.

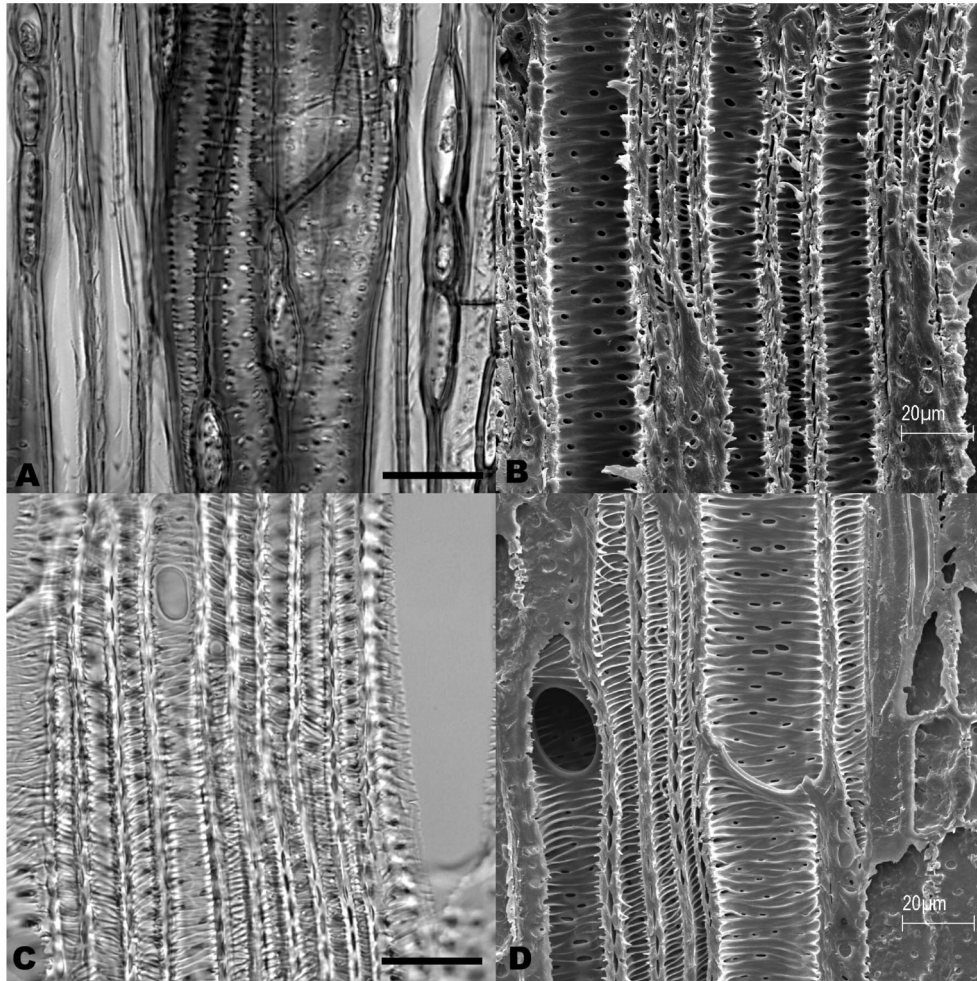


Fig. 4. Helical thickenings in the vessel elements of *Croton alabamensis* and *C. fruticosus* seen with light and scanning electron microscopy. (A, B) *Croton alabamensis* var. *alabamensis* (van Ee 365). (C, D) *C. fruticosus* (Dechamps 4112). Scale bars = 20 μ m. In *C. alabamensis* the helical thickenings are more tooth-like in their nature and are less organized than those seen in *C. fruticosus*.

We suggest that HT may well not be needed for resisting conduit collapse in dry conditions (Hypothesis 1), but rather for re-establishing the transpiration stream during the transition from dry to wet conditions (Hypothesis 2) and/or increasing the efficiency of water conduction (Hypothesis 3), especially in taxa wherein conductive elements experience an ecophysiological (e.g., freezing-induced embolism) ontogenetic (e.g., latewood vessel diameter), or phylogenetic (e.g., maximum tracheid diameter in gymnosperms) constraint limiting diameter. This suggested function is supported by the fact that other than in mediterranean-type climates, most species with HT are found in mesic environments or temperate latitudes (Wheeler & Baas 1993), and within taxa bearing HT with a wide latitudinal range, HT tend to be more abundant or prominent at higher latitudes (e.g., in *Ilex* (Baas 1973) or in *Acer* (Regis Miller, personal communication)). In such climates, cavitation and embolism are essentially guaranteed over the functional lifetime of a growth increment of wood, therefore vessel refilling would be likely to be a critical parameter for the long-term hydraulic safety of the plant (Sperry & Tyree 1988; Holbrook & Zwieniecki 1999), especially for taxa with narrower and thus less efficient conduits and ring-porous taxa, wherein earlywood conductivity is lost during the growing season (Zimmerman 1983).

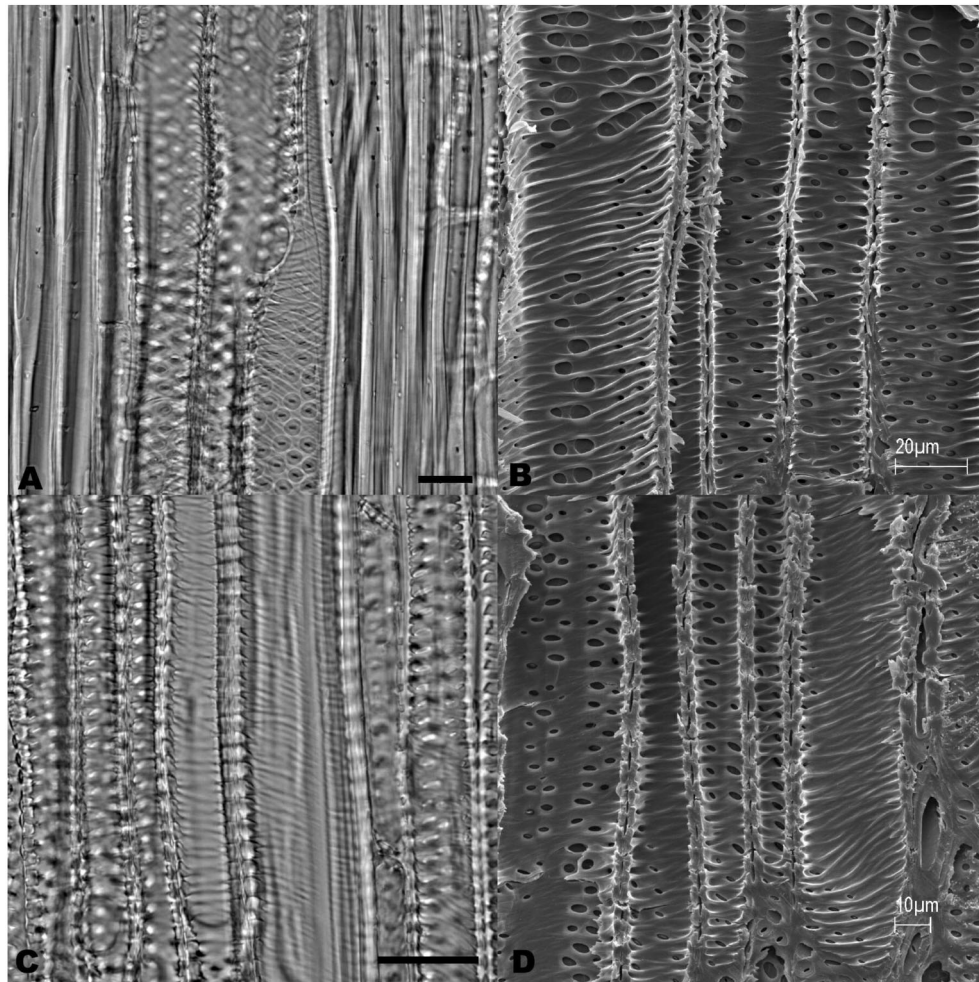


Fig. 5. Helical thickenings in the vessel elements of *Croton flavispicatus* and *C. lanatus* seen with light and scanning electron microscopy. (A,B) *Croton flavispicatus* (Belgrano 395). (C,D) *C. lanatus* (Belgrano 398). Scale bars = 20 μ m. Both the light (A, C) and scanning electron (B, D) micrographs show the presence of helical thickenings throughout the body of the vessel elements.

Conduit refilling broaches the topic of HT as implicated in conduit wettability (Jeje & Zimmerman 1979; Holbrook & Zwienicki 1999; Kohonen 2006; Wiedenhoef 2008; Kohonen & Helland 2009; Lens *et al.* 2011) whether to increase hydrogen bonding to the lumen surface to presumably resist cavitation (Carlquist & Hoekman 1985, though see Lens *et al.* 2022 for updated thoughts on this mechanism), or in relation to conduit refilling as a part of embolism recovery. This hypothesis, if true, could explain the presence of HT throughout the body of a vessel element as well as the presence of HT restricted to the tails of vessel elements. The latter is not a part of the direct perforation plate-to-perforation plate hydraulic pathway, so their function cannot reasonably be attributed to bulk flow in the transpiration stream.

It was suggested by Wiedenhoef (2008, unpublished thesis), Arévalo *et al.* (2017), and is reiterated here that HT in the tails of vessel elements may be implicated in the efficient refilling of embolized vessels, which would be consistent with the results of Brodersen *et al.* (2018) showing, generally, that smaller-scale anatomical features with connectivity to adjacent parenchyma show evidence of water accumulation into vessels, compared to larger-scaled features. This was essentially predicted by Zwieniecki & Holbrook (2000), who showed that the geometry of intervessel pit borders

and chambers could affect the likelihood of air-seeding and the maintenance of positive pressures necessary for vessel refilling. Similarly, Kohonen (2006) and Kohonen & Helland (2009) posited a vessel wall wettability argument for lumen wall relief as a function of contact angle. The angles of the cell wall in a vessel element tail, particularly one with HT, provide a similarly favorable geometric environment in which water can be retained by capillary forces in spite of cavitation in the body of the vessel element. The small volume of vessel element tails would also make them well-suited to rapid osmotic modification by the secretion of solutes by adjacent parenchyma cells, thus rapidly lowering the water potential of the water in the tail, and so providing the initial motive force for vessel refilling. Inasmuch as the vessel element tails are not a part of the normal transpiration pathway, bulk flow of solutes out of the region of the tail would be slower, and so higher water potential gradients could be maintained with a lower cost in solute translocated to the transpiration stream. Diffusion of solutes into the body of the vessel element would be slower than the bulk flow and mixing that would occur within the body of the element. Furthermore, when HT extend either throughout the vessel element (Figs 4 and 5) or from the tails of the vessel element slightly into the body (Fig. 3), it is possible that HT could facilitate capillary flow along the wall of the vessel by virtue of enhanced wettability (Hypothesis 2). Interestingly, in contrast to Lens *et al.* (2011) report for HT in *Acer*, in *Croton* the helices clearly pass through areas with intervessel pits (Figs. 3, 4 and 5), as well as vessel-parenchyma interfaces. If the solute volume hypothesis were true, helices on the vessel-parenchyma faces could also allow for narrow channels of high solute concentration early in conduit refilling.

This composite hypothesis, while not directly related to the wood anatomical character evolution of *Croton*, does account for the distribution of this character across various groups, and could be extended to most woods. It is also consistent with the demonstrated associations between aliform parenchyma and mesic and especially tree *Croton*; aliform (or any paratracheal) parenchyma would be available for osmoregulation of the transpiration stream, particularly for generating positive pressures in embolized vessels.

The last hypothesis (No. 3) for the function of HT is to increase flow rate/conductivity or reduce hydraulic drag. Note that this function would be restricted to thickenings in the main hydraulic pathway of the conducting cells, that is, not in HT restricted to vessel element tails or tracheid tips. Jeje & Zimmerman (1979) presented limited experimental evidence to suggest that vessels with HT conducted water more rapidly under capillary driving forces with an air-water interface than those that lack HT. Wang (2006) demonstrated that for low Reynolds numbers, conduits with helical corrugations can have optimal relationships between corrugation size, angle, and spacing to induce rotational flow, lower resistance, and thus maximize flow rate. It is critical to note that such an explanation is only defensible if the percent increase in conductivity as a result of HT is high, or if there is some other constraint to conduit diameter. To wit, if HTs were to give a 10% increase in conductivity at a given conduit diameter, the proportional increase in conduit diameter to achieve the same flow rate is an increase of only 2.4% — in a conduit with a diameter of approx. 40 μm , that is only an increase in diameter of approx. 1 μm . For the same size conduit, a 100% increase in efficiency only amounts to approx. 18% diameter increase (approx. 7 μm), a 200% increase to approx. 31% (approx. 12 μm), and a 300% increase to approx. 41% (approx. 16 μm). Thus, for HT to be implicated in increased flow rate/reduced hydraulic drag or resistance, we presume that there must exist some other limit on conduit diameter (e.g., developmental constraints in *Pseudotsuga menziesii* or in the latewood of ring-porous hardwoods; freeze-thaw embolism risk in temperate mesic diffuse-porous taxa, or organographic or allometric constraints, e.g., in shrubby taxa) such that increasing vessel diameter to improve flow is not possible or is otherwise deleterious.

It is also interesting to note that, in general, larger diameter vessels lack HT, both within a wood (e.g., in ring-porous woods with HT where they are restricted to the latewood), and across taxa. We presume that, regardless of the function in a given wood, there must be some critical diameter (as in Echeverría *et al.* (2022) with vessel diameter and wall thicknesses) above which the value of HT becomes negligible, whether mechanically, for wettability, in the context of conductive efficiency, or for as-yet unknown functions.

It is our sincere hope that researchers in experimental physiological wood anatomy and comparative wood anatomy will consider these hypotheses and explore ways in which they can be tested. The breadth and depth

of woody taxa in which HT are found certainly suggest the roles HT play in wood are significant, diverse, and consequential. We further assert that the full range of possible roles or functions of HT may well not have yet been hypothesized, let alone tested, refuted, or supported. It is simultaneously refreshing, inspiring, and maddening that a wood anatomical feature known for centuries remains so incompletely understood, and we look forward to a future where it is better studied.

Conclusion

HT are features classified under the umbrella of vessel wall sculptures that have been observed in plants for centuries, with various and progressively changing interpretations of their functions, especially in wood. Dr. Carlquist was among the first wood anatomists to posit functional roles for HT in conductive cells in wood and to demonstrate associations between HT (and other forms of vessel wall sculpture) and conditions of water stress created by either drought or cold (physiological drought). He explicitly identified the probability that vessel wall sculpture could serve different functions in different woods, and though he did not emphasize it strongly, it is clearly one of the compelling instances of convergent evolution in wood anatomy.

We summarize three functional hypotheses previously proposed for the presence of HT in conductive elements. The biomechanical hypothesis suggests that the function of HT is to provide additional mechanical support and strength to the conducting elements to resist implosion, especially in environments where high xylem tensions occur. The refilling hypothesis suggests that HT increase lumen wall wettability by providing favorable contact angles. Some researchers have suggested that this would result in fewer cavitations, whereas we suggest it would be implicated in improved conduit refilling. Lastly, a hypothesis founded in theoretical fluid dynamics suggests that optimal HT geometry could induce rotational sap flow that lowers flow resistance and thereby increases flow rate.

In an attempt to review the past and present interpretations of the functions of HT in wood, and further to make some suggestions for future work, we endeavored to engage in a critical revisitation of the literature and presentation of data from a pantropical genus, *Croton*, in which HT are associated with mesic rather than xeric conditions. Based on these observations, we found no concrete evidence to support the hypothesis that HT provide vessel-collapse resistance in seasonally dry environments in *Croton*. We suggest that HT may exist to support two related functions; vessel refilling following cavitation, and increased hydraulic efficiency, with the latter most prominent when other constraints limit conduit diameter. We believe that structure-function relationships and evolutionary paths of HT offer myriad potential research opportunities, and we encourage our colleagues to pursue research that will elucidate the function(s) of HT in wood.

Survey data of wood anatomical patterns

Data on helical thickenings and geographic origin for woods worldwide were downloaded from InsideWood (2004 onward) and compiled in Excel. In all cases, searches were limited to the set of taxa bearing vessels (e.g., feature 59 wood vesselless defined as absent), resulting in a set of 7696 records in total, of which 2135 were temperate and 5561 were tropical. Tropical regions, for the purposes of the summary data, were defined as the total number of taxa in the database minus the sum of those in Eurasia (Brazier & Franklin zone 74), North America (Brazier & Franklin zone 80), temperate South America (Brazier & Franklin zone 82) and New Zealand (Brazier & Franklin zone 77), as grouped by IAWA Committee (1989).

Acknowledgements

We would like to thank João do Marco for his diligent work to evaluate helical thickenings in a range of taxa in the context of Wang's fluid dynamic work (data not shown). Special thanks to Phil Jenkins at ARIZ for small stem specimens from vouchers of *Croton*. Our sincere thanks to Dr. Mark Olson and the anonymous reviewer, whose invaluable feedback has greatly improved the quality of this manuscript. This paper was approved as journal article SB1083 of the Forest & Wildlife Research Center, Mississippi State University.

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Edited by Marcelo R. Pace