

WOOD POROSITY AS AN ADAPTATION TO ENVIRONMENTAL CONDITIONS

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ABSTRACT: Woody plants are categorized as non-porous, diffuse-porous, and ring-porous, on the basis of anatomical features of their water conducting system. Based on the anatomical differences, the softwood and hardwood species differ in degree of their vulnerability to disturbance in sap flow. Despite suffering from cavitation and embolism, ring-porous and diffuse-porous trees adopt different mechanisms to restore their conductivity after winter frosts. This also applies to specific ways of gaining appropriate functionality at the beginning of a new growth season. Mechanisms of restoring water conduction are related to production of new conduits characterized by high efficiency, or recovery of non-functional vessels. Both strategies require different usage of carbon reserves, which may accumulate during the growing season. Although plants are able to adapt to unfavorable environmental conditions, there is always a threshold beyond which adaptation is not feasible. In this situation a disturbing factor, such as cavitation, may become a limiting factor for the natural distribution of plants.

KEY WORDS: ring-porous, diffuse-porous, non-porous, strategies, distribution.



Introduction

Water is a crucial factor determining the existence of life on Earth. While colonizing terrestrial environment, plants were forced to develop mechanisms for efficient uptake and transport of water in varied environmental conditions. During the active transpiration, a suction force is generated (by differences of water potential between soil solution, plant interior and the atmosphere), inducing the ascent of sap. Continuity of the water column is maintained by the presence of cohesion and adhesion forces. Unfavorable changes in external conditions can interrupt sap flow in plant axis and ultimately lead to death of the plant. Plant adaptation to different environmental conditions requires various strategies.

This article aims at characterizing differences in anatomical structure of tracheary elements in relation to periodical fluctuations in water availability and temperature. It also describes different adaptation strategies and seasonal dynamics of carbon reserves. In order to familiarize the reader with issues at hand, basic information about cavitation and embolism, the major phenomena affecting the flow of water, has been incorporated. Strategies used by coniferous and deciduous trees for adaptation to environment, and differences in the functioning of ring- and diffuse-porous species, have been discussed, paying attention to relationship between climatic limitations in geographical distribution of plants and cavitation of vessels.

Wood structure in non-porous, diffuse-porous, and ring-porous trees

Coniferous wood is characterized by a relatively homogenous structure: small diameter tracheids (as opposed to angiosperm vessels), small amount of axial and ray parenchyma, and (in some genera) epithelial cells surrounding resin ducts. Dicotyledonous wood structure is much more diversified. It is typically composed of

tracheids, vessel elements, fibers, axial parenchyma and ray parenchyma (Esau 1965; Evert 2006).

Coniferous wood can be classified as non-porous, for it does not contain vessels, i.e. no pores in a transverse section (IAWA COMMITTEE 1989; Phillips et al. 1996; Rowell 2005; Evert 2006; Beck 2010). One can distinguish two main porosity types in the wood of deciduous trees: ring-porous and diffuse-porous. There are also intermediate types: semi-ring-porous or semi-diffuse-porous wood (Evert 2006; Pan and Kudo 2012). All these structural forms are distinguished on the basis of cross-sectional differences in vessels' size and distribution within growth rings.

In ring-porous wood very broad vessel elements occur exclusively in earlywood (springwood), whereas fiber tracheids and wood fibers of narrow lumen prevail in latewood (summerwood) (Brown et al. 1949) as, for instance, in *Castanea*, *Catalpa*, *Celtis*, *Fraxinus*, *Gleditsia*, *Morus*, *Paulownia*, *Quercus*, *Robinia* and *Ulmus* (Evert 2006). In diffuse-porous wood vessels are uniformly distributed across the growth rings and their diameters do not change significantly between earlywood and latewood, e.g. in *Acer*, *Aesculus*, *Alnus*, *Betula*, *Carpinus*, *Cornus*, *Fagus*, *Liriodendron*, *Magnolia*, *Platanus* and *Tilia* (Evert 2006). The intermediate type of wood porosity occurs in such genera as *Diospyros*, *Juglans*, *Populus*, *Prunus*, *Quercus* and *Salix* (Evert 2006). Porosity type is not necessarily the same throughout an individual tree. Broad vessels typically occur in above-ground parts of the plant. Individual specimens may have different porosity type in case of roots. Ring porosity may change gradually into diffuse porosity towards root endings, or earlywood vessels in root may not be as distinct from latewood vessels as in the stem (Tsoumis 1968; Kedrov 2012).

Processes related to sap flow

Proper development and functioning of plant require an efficient conduction of sap. Disruption of water column (under tension) may lead to xylem transport failure (Domec et al. 2009). One of the phenomena that has a significant effect on conductivity is cavitation, i.e. transition of water from liquid to vapor phase, in xylem conduits under negative pressure – during intense transpiration. This phenomenon may arise in both vessels and tracheids. Such cells may be completely filled with air that gradually expands, which is called the embolization. In that case, tracheary elements lose their conductive capacity (Tyree and Sperry 1988, 1989). During the initiation of cavitation the pressure in a xylem vessel increases instantaneously to vapour pressure of water, thus there exists a higher water potential in the cavitating compartment. The resulting gradient of water potential induces a flow of water from conduits affected by the disturbance to adjacent functional cells (Oertli 1993). This movement occurs through pit pairs. Pit pairs between different types of wood cells may be simple, half-bordered or bordered. The last type, characterized by the curvature of secondary wall towards cell lumen, occurs between tracheary elements. The middle lamella and primary walls of adjacent elements form the pit membrane. With this type of connection, angiosperms with secondary growth may attain three-dimensional vascular network organization (Kitin et al. 2004). The same is true for the gymnosperms where this organization stems not only from pits on lateral walls but also from overpositioning of tracheid ends, which – in the neighboring radial rows – are located at different heights in reference to the main stem axis (non-storeyed arrangement) (Kedrov 2012).

The radial and longitudinal transport is characterized by flow resistance. Effectiveness of longitudinal flow is determined, *inter alia*, by length and diameter of a vessel (Ahmed and Chun 2011), and the resistance itself – imposed

by the type of perforation plate and interaction with cell wall (Ellerby and Ennos 1998). Recent studies indicate that resistance imposed by scalariform perforation plate (as opposed to simple perforation) was underestimated (Christman and Sperry 2010). Radial transport, which occurs through the pit membranes (Fujii et al. 2001), is approximately six orders of magnitude lower than the longitudinal one (Zwieniecki et al. 2001), which explains smaller conductivity of water in radial direction. Significant flow resistance, imposed by pit pairs, has been frequently measured and calculated by many researchers (Choat et al. 2006; Xu et al. 2012). Nevertheless, pits also have a second function, which is essential to ensure the safety of water conduction. Due to surface tension at water-air meniscus between the functional and embolized vessels, pit pairs prevent gas spreading to the neighboring, functional conducting cell. However, if increased negative pressure in xylem conduits (as a result of reduced water availability) exceeds surface tension, the air will be pulled into the functioning vessel (Evert 2006). The role of pit pairs in air spreading has been highlighted by numerous studies (Sperry and Tyree 1988; Sperry et al. 1991). Old vessels with degraded pit membranes have an increased susceptibility to spread of air (Sperry et al. 1991).

Pit pairs in coniferous and deciduous species, despite having the same function, differ in structure and thus in the strategy of maintaining hydraulic conductivity. Contrary to the angiosperm pits with homogenous membranes, conifer pits have two clearly distinct areas of pit membrane: a thickened, centrally-located torus and a porous, peripheral margo (Choat and Pittermann 2009). The homogenous pit membranes in angiosperms, bearing small pores, provide high resistance to the possible spread of air. In contrast, coniferous membranes with large margo pores allow greater flow of water, which compensates small length of

tracheids in comparison with long angiosperm vessel conduits. Flow security is ensured by margo flexibility, which makes adherence of impermeable torus to pit aperture possible (Pittermann et al. 2005). In such a case, seeding of air may be caused by incomplete adherence of torus to pit aperture (Delzon et al. 2010). Contrary to the widespread assumption that torus is impermeable, a recent report describing some conifers indicates the presence of pores in torus, which could let the air through. Species having that type of torus are less resistant to air seeding (Jansen et al. 2012). Vulnerability to air seeding is determined not only by the size of pores, but also by other structural features of pit pairs. Species belonging to Cupressaceae showed a correlation between cavitation resistance and the ratio of torus to pit aperture diameter (Pittermann et al. 2010). As reported by Lens et al. (2011), pit resistance to cavitation is associated with membrane thickness and pit-chamber depth in *Acer* species. Plants tend to prevent cavitation and progress of air seeding by developing mechanisms (such as closing the stomata to reduce loss of water) to adapt to dry and arid environments, and repairing damage caused by cavitation (Jones and Sutherland 1993).

Cavitation occurs not only in conditions of water stress, but also as a result of frost (Utsumi et al. 1998, 1999; Willson and Jackson 2006; Cobb et al. 2007) as well as wounding and parasitic infections (Newbanks et al. 1983; Umebayashi et al. 2011). Sap contains dissolved gases in equilibrium with their concentration in the atmosphere. Interruption of the continuity of water flow due to freezing and thawing of xylem sap is a consequence of different solubility of those gases in water and ice. When water freezes, gas solubility decreases rapidly and small bubbles are excluded from the crystal structure of ice (Utsumi et al. 1999; Cobb et al. 2007). These bubbles enlarge and cause embolism, if their initial diameters and tension force generated in vessels are large enough. The wider the vessel,

the larger the air bubbles and the greater the probability of flow dysfunction (Sperry and Sullivan 1992; Sperry 1993). Considering the positive correlation between vessel diameter and vessel susceptibility to frost-induced cavitation (Sperry and Sullivan 1992; Tyree et al. 1994), it is noteworthy that species having smaller vessels usually have them grouped in clusters (Gutiérrez et al. 2009), because clusters tend to decrease negative effects caused by conduits dysfunction (Lens et al. 2011).

Moreover, resistance to cavitation is influenced by the amount of vessel grouping and the degree of helical thickening formation on the inner vessel surface (Lens et al. 2011). Populations of *Ephedra* species growing in cold areas (high elevations and high northern latitudes) had vessels and tracheids with more pronounced helical thickenings (Carlquist 1989, 1992). It may be emphasized that the pattern of development of many structural features of xylem often varies within a given plant. Frequency of narrow vessels in the wood increases towards the tree crown (Zimmermann and Potter 1982; Aloni and Zimmermann 1983; Aloni 1989). Hacke and Sauter (1996a) examined vulnerability of various plant organs to cavitation and found the highest sensitivity in roots. Nevertheless, various buffering mechanisms associated with storage of water may possibly work against cavitation-inducing pressure (Meinzer 2003; Meinzer et al. 2003). Vulnerability to cavitation seems to increase with vessel aging (Melcher et al. 2003).

The loss of functionality of conducting cells is not always definitive. Greater part of sapwood is able to participate in water transport by means of conductance-restoring mechanisms (Holbrook and Zwieniecki 1999; Holbrook et al. 2001; Vesala et al. 2003). Refilling xylem conduits with sap can occur repeatedly, allowing plant survival. Daily cycles of embolism and refilling were observed, e.g. in *Zea mays* L. (McCully 1999). Recovery of hydraulic

conductivity may occur despite the existence of negative pressure within the xylem (Stiller et al. 2005); however, generation of positive pressure in an embolized conduit is necessary for gas dissolution. It is assumed that parenchyma cells participate in the process, actively pumping substances into an embolized vessel. Increase of osmolarity results in the flow of water into non-functional conduit. As Holbrook and Zwieniecki (1999, 2000) concluded, refilling is enabled by pit-pair structure and hydraulic isolation resulting from lignification of tracheary elements' walls. The flow of water into refilled vessel, by means of aquaporins localized in plasma membranes of parenchymatous cells, has been suggested in various studies (Holbrook and Zwieniecki 1999; Zwieniecki and Holbrook 2000; Sakr et al. 2003). Model calculations support the view that the process of recovery is possible if the adjacent vessels, being under tension, are in hydraulic isolation from refilling vessel (Vesala et al. 2003). Active osmosis theory was also proposed for coniferous trees affected by cavitation caused by freezing (Grace 1993). Generation of positive pressure is also important in case of these gymnosperms. Therefore, during rapid thawing, dissolution of bubbles is possible before the occurrence of intensive transpiration. Negative pressure inside the vascular system is created after intensive transpiration has set in. Pressure gradient exists between thawing and functional tracheid. Adhesion of torus to pit aperture maintains the difference of pressures, and hydraulic isolation of thawing cell allows for gas dissolution (Robson and Petty 1993). Moreover, root pressure is considered to participate in restoring hydraulic conductivity (Sperry et al. 1994; Utsumi et al. 1998). Contribution of root pressure has been elucidated with reference to *Acer saccharum* Marshall (Sperry et al. 1988), *Betula cordifolia* (Reg.) Fern. (Sperry 1993), *Fagus sylvatica* L. (Cochard et al. 2001), *Juglans regia* L. (Améglio et al. 2002), and *Vitis riparia* Michx. (Sperry et al. 1987).

Plant survival strategies versus environmental conditions

Trees growing in tropical rain forests

Plants exhibit a variety of strategies associated with adaptation to unfavorable environmental conditions such as frost and drought. These survival strategies are based on avoidance or extended tolerance of adverse factors. Tropical rain forests offer almost perfect conditions for plant growth. Limiting factors, such as water stress or low temperature, are practically absent (Kojas et al. 2003). Leaves are continuously present on trees throughout the year. Tropical species may maintain radial increment all year round (Alves and Angyalossy-Alfonso 2000), although in some cases seasonal increment requires rainfall (Kozłowski 1965; Venogupal and Kirshnamurthy 1987; Dünisch et al. 2002; León-Gómez and Monroy-Ata 2005; Marcati et al. 2006; Westbrook et al. 2006). Growth rings, typical for trees growing in temperate climate zones (Priestley 1930; Brown 1935; Frankenstein et al. 2005), or more generally, where some kind of seasonality (e.g. seasonal rainfalls) occurs (Kozłowski 1965; Venogupal and Kirshnamurthy 1987; Dünisch et al. 2002; León-Gómez and Monroy-Ata 2005; Marcati et al. 2006; Westbrook et al. 2006), are predominantly absent in tropical trees due to lack of seasonal changes (Alves and Angyalossy-Alfonso 2000). In areas characterized by periodicity of climatic conditions, wood increment occurs only during the growth season (Lipshitz et al. 1984; Deslauriers et al. 2008). It may be mentioned that in tropical rain forests, where light deficit is one of the most important limiting factors (Kojas et al. 2003), it is crucial for trees to have a highly efficient water conducting system in order to sustain a fast longitudinal growth. In trees of emergent layer, there often occurs a specific figure – interlocked grain – which contributes to strengthening of tree trunk, while maintaining a relatively small circumference of the trunk (Kojas et al. 2002, 2003). Tree species growing in

tropical climate have diffuse-porous wood with very large vessel diameters (Fig. 1a), in comparison to diffuse-porous trees of temperate climate zones (Fig. 1b). It appears as if, in the absence of drought- and frost-induced cavitation, tropical trees have developed the least expensive and the most efficient water-conducting system. In tropical wood with large-diameter vessels that remain functional for several years, water transport is so efficient that there are only few vessels. Representative tangential (minimal–average–maximal) vessel diameters in tropical trees are: 155–265–320 μm (*Millettia laurentii* De Wild.), 200–250–280 μm (*Triplochiton*

scleroxylon K. Schum.), and 155–200–245 μm (*Antiaris toxicaria* Lesch.), in contrast to tangential vessel diameters in temperate diffuse-porous trees: 40–60–90 μm (*Alnus* spp.), 30–90–130 μm (*Betula* spp.), and 44–65–80 μm (*Acer* spp.) (Richter and Dallwitz 2000). Temperate ring-porous species are characterized by large diameter earlywood vessels (minimal–maximal): 250–300 μm (*Catalpa bignonioides* Walt.), 200–300 μm (*Paulownia tomentosa* Steud.) (Richter and Dallwitz 2000). It is noteworthy that vessels of tropical species have diameters comparable to earlywood vessels of ring-porous ones.

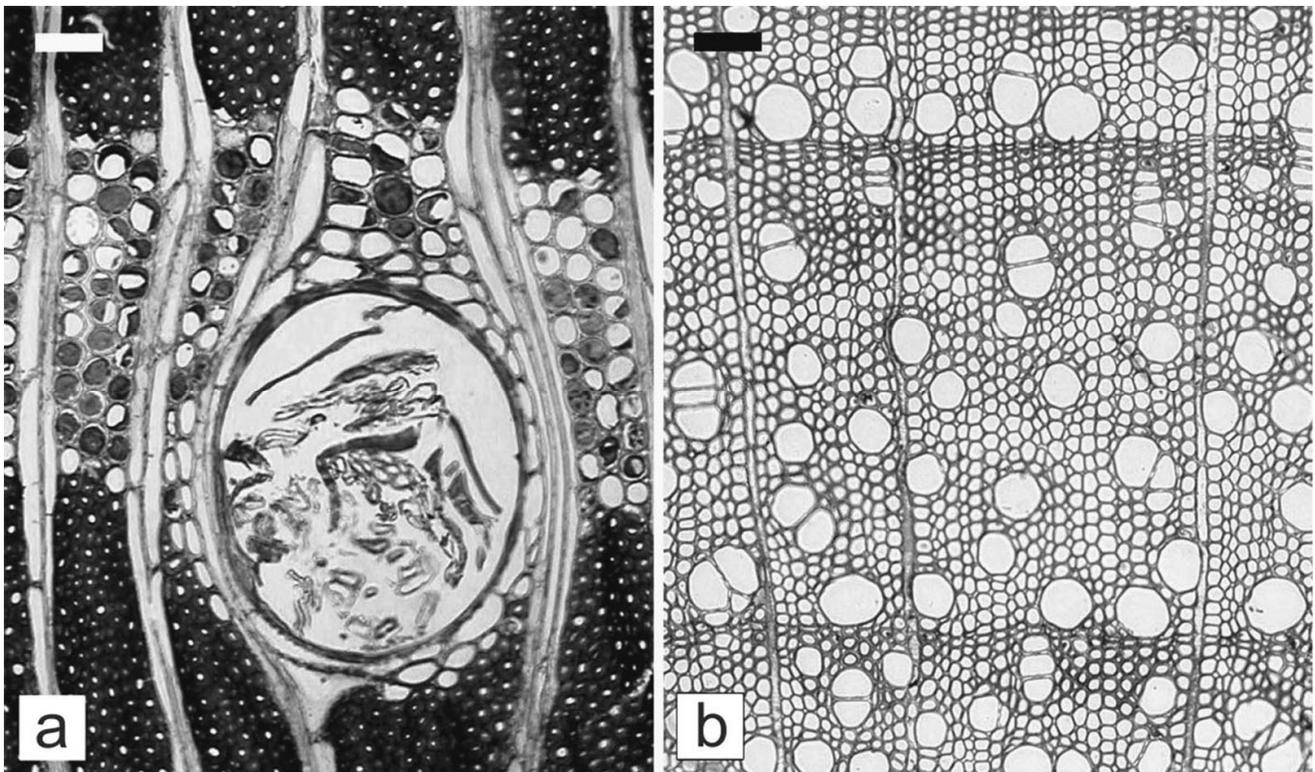


Fig. 1. Transverse sections of diffuse-porous wood. **a** Mature wood of *Lonchocarpus sericeus*. **b** Juvenile wood of *Acer platanoides*. - Scale bar = 50 μm .

Trees growing outside tropical rain forests

We presume that the system of water transport in tropical rain forest trees is safe enough, but in temperate climate zones it would be dysfunctional due to high risk of cavitation and embolism, related to large diameter of their vessels. During the course of evolution, in order

to conquer other climates and habitats, trees had to adjust to different environmental setups in the best possible way. It seems that smaller diameters of tracheary elements, more resistant to frost-induced cavitation (Utsumi et al. 1999; Pittermann and Sperry 2006), developed during

trees' acclimatization to colder climates (moving further from the Equator).

It appears that developing ring-porous wood is a very specialized adaptation to specific climate conditions, and it is partly related to frost-induced cavitation.

In spite of similar, harmful consequences of cavitation and embolism, ring-porous and diffuse-porous trees harness radically different mechanisms enabling them to recover their conductivity after winter frosts (Cochard and Tyree 1990; Sperry and Sullivan 1992; Sperry 1993; Sperry et al. 1994; Hacke and Sauter 1996b; Utsumi et al. 1996, 1998, 1999; Tibbetts and Ewers 2000). This also refers to specific ways of obtaining an appropriate functionality at the beginning of a new growth season. The following discussion analyzes all these strategies adopted by different groups of trees, including conifers.

Non-porous trees

In conifer wood the freezing of sap may occur without causing cavitation (Hammel 1967; Davis et al. 1999). The main feature of wood allowing coniferous trees to endure multiple freeze-thaw cycles and restrict embolism levels at about 10–30 % is the small diameter of tracheids (in comparison to vessels of deciduous trees) (Sperry et al. 1994). This is why gymnosperms are not highly threatened by frost-induced cavitation (Sperry and Sullivan 1992; Davis et al. 1999; Pittermann and Sperry 2003). Nevertheless, transport efficiency may be reduced by limited water uptake from the frozen soil (Sperry 1993). Comparatively small diameters of conifer tracheids are considered to contribute to better survival of trees in low temperatures (Sperry and Sullivan 1992). In the case of angiosperms positive relationship is said to exist between hydraulic efficiency (related to vessel diameter) and mean annual temperature (Zhang et al. 2013). Given the above, it can be assumed that small diameter of tracheids may be the reason

why conifer trees predominate in taiga forests (Barbour and Billings 1988; Perry 1994).

Conifers might reverse embolism by refilling tracheids, utilizing embolism repair mechanisms described above. Conifer tracheids are superior to vessels in avoiding freeze-thaw-induced embolism (Sperry et al. 1994). As water has to pass through bordered pit-pairs in tracheid cell walls, it is believed that such a structure of wood makes for the low velocity ascent of sap (Evert 2006), in comparison to angiosperm wood. However, the structure of conifer pit membranes partly compensates this loss in efficiency of water transport (Pitterman et al. 2005). Interestingly, pine trees in response to drought stress form larger tracheids (Maherali and DeLucia 2000; Eilmann et al. 2009; Eilmann et al. 2011) with thinner cell walls, which provide more effective water conduction. Having thinner cell walls, however, does not cause them to lose the ability to recover from drought-induced embolism (Eilmann et al. 2011).

Diffuse-porous trees

Regaining hydraulic conductivity in diffuse-porous trees after winter period has been studied extensively (Sperry et al. 1988; Sperry 1993; Sperry et al. 1994; Hacke and Sauter 1996b; Utsumi et al. 1998; Cochard et al. 2001). In *Betula platyphylla* var. *japonica* and *Salix sachalinensis* Fr. Schm. cavitation starts in December and reaches its maximal level in March, rendering about 80% and 70% vessels embolized in the two species respectively (Utsumi et al. 1998). However, in diffuse-porous wood, prior to leaf emergence and transpiration commencement, most of the embolized vessels regain their function by means of the refilling process (Sperry et al. 1994; Utsumi et al. 1998). Cavitation and refilling occur repeatedly, up to several years, until embolism becomes irreversible (Utsumi et al. 1998). However, the general loss of hydraulic conductivity in diffuse-porous trees is less extensive than in ring-porous

ones (Sperry 1993; Hacke and Sauter 1996b; Sperry and Sullivan 1992).

Ring-porous trees

In case of ring-porous trees water transport functions are maintained in the latewood of several outermost annual growth rings, whereas large earlywood vessels maintain this function only in the outermost ring, located adjacent to the vascular cambium. It is precisely this growth ring, which is responsible for over 90% of water transport in xylem in this type of wood (Kozłowski and Winget 1963; Sperry et al. 2006). Thus, earlywood vessels remain functional only for one growth season – the one they were produced in (Ellmore and Ewers 1986). It was observed that earlywood vessels abruptly lose their conductivity after the first frost (Cochard and Tyree 1990; Sperry and Sullivan 1992; Sperry et al. 1994; Hacke and Sauter 1996b; Utsumi et al. 1996; Utsumi et al. 1999; Tibbetts and Ewers 2000). Precise examinations with use of cryopreservation revealed only small air bubbles in xylem sap of earlywood vessels during winters. Abrupt expansion of air bubbles occurred on the first day after thawing, causing lost of hydraulic functionality (Utsumi et al. 1999). Similar results for ring-porous trees were obtained by Wang et al. (1992) and Sperry and colleagues (1994). Although the results of Taneda and Sperry (2008) suggest that ring-porous oak refilled embolized vessels overnight during most of the summer, the refilling process apparently stopped in early fall. Latewood vessels provide slower but continuous and reliable water transport (Cochard and Tyree 1990; Hacke and Sauter 1996b; Utsumi et al. 1999; Jaquish and Ewers 2001) and remain functional in several successive growth seasons (Zimmermann 1983; Ellmore and Ewers 1986; Cochard and Tyree 1990; Utsumi et al. 1999; Jaquish and Ewers 2001). These are less susceptible to freeze-thaw-induced cavitation (Hacke and Sauter 1996b;

Jaquish and Ewers 2001). When cavitation develops in broad earlywood vessels of ring-porous trees, latewood vessels, having relatively smaller diameters, should still participate in water transport (Zimmermann 1983; Ellmore and Ewers 1986; Cochard and Tyree 1990; Hacke and Sauter 1996b; Utsumi et al. 1999; Jaquish and Ewers 2001). Very interesting studies concerning secondary xylem vessel network were conducted by Kitin et al. (2004), who showed that vessels, which seemed to be solitary on a single transverse section, were in fact sequentially contiguous with neighboring vessels, thus forming network extending in a tangential direction. These connections were very abundant between earlywood vessels and previous year's latewood vessels, i.e. across growth-ring boundaries, although such vessel connections have been described as sparse by Kedrov (2012). In both these examinations (Kitin et al. 2004; Kedrov 2012), only few connections were observed between earlywood and latewood vessels within a growth ring. Lens and colleagues (2011) showed that the amount of intervessel connectivity is not associated with the vessel grouping index, suggesting that wood with solitary vessels and radial vessel multiples shows similar amounts of intervessel overlap. Taking into consideration that a single vessel of large diameter in ring-porous trees can reach the length of several meters (Esau 1965; Zimmermann and Jeje 1981) and exhibits strong deviations in circumferential direction (Zimmermann 1983; Wilczek et al. 2011), existence of connection among all vessels in one functional network seems to be very reasonable. It would be interesting to test the hypothesis that the existence of such a network can be associated with providing water to newly formed earlywood vessels of ring-porous trees. It has been shown that spatial arrangement of vessels indeed influences functioning of the network (Martínez-Vilalta et al. 2012). Nevertheless, more research is required to further elucidate the subject.

Apart from the role of latewood vessels, it is speculated that fibers also contribute to water transport by providing water outlet from embolized vessels via direct migration to fibers or indirectly with the help of parenchyma cells (Utsumi et al. 1999). An interesting case was described by Cobb et al. (2007), who examined a monocotyledonous vine – *Smilax rotundifolia*, which does not exhibit secondary growth. This plant is characterized by the presence of large-sized metaxylem vessels, similar to those in the earlywood of some ring-porous species. It is no surprise that vessels of *S. rotundifolia* succumb to embolism during rapid temperature decrease. Due to the absence of vascular cambium it is impossible for the plant to use the ring-porous trees strategy. The hydraulic conductance is regained before spring by generation of strong root pressure, and possibly by increase of hydrostatic pressure contributing to gas vesicles dissolution (Cobb et al. 2007).

Carbon reserves and seasonal activation of cambium

Another vital step leading to more complete comprehension of how trees with different wood porosity type cope with drought-induced and frost-induced loss of conductivity is related to the maintenance and dynamics of reserve substances. In tropical evergreen trees, leaves are produced in a stable and uninterrupted manner and cambium may remain active continuously (León-Gómez and Monroy-Ata 2005; Yáñez-Espinosa et al. 2010). However, if dry and moist seasons alternate, cambial activity may change seasonally, especially if a tree produces new foliage periodically (Iqbal and Ghouse 1985; Iqbal 1994, 1995; Rao and Rajput 1999; Evert 2006). This indicates the importance of water in radial growth phenomenon, which is confirmed by a strong correlation between growth ring width and water availability (Abe and Nakai 1999; Wimmer et al. 2002; Campelo et al. 2007; Eilmann et al. 2009). In order to understand the

process of producing a new annual increment (cell wall components and other structures) of wood, it is worthwhile to examine how the non-structural carbon (C) reserves are maintained and utilized throughout a year.

Zweifel et al. (2006) reported large growth increment before bud break, i.e. before the beginning of transpiration, in *Quercus pubescens*. In two conifers, *Pinus sylvestris* and *Picea abies*, which remained photosynthetically active during winter period, excluding moments when low temperature caused water freezing, radial growth inception took place approximately two weeks later than in *Q. pubescens*. Radial growth in ring-porous species began 3–5 weeks before foliage development, thereby before the first carbon-molecule assimilation. In that period, a tree was totally dependent upon previously accumulated C reserves (Zweifel et al. 2006). A study conducted on *Castanea sativa* Mill. also led to the same conclusion (Čufar et al. 2011). Coniferous species are able to assimilate C long before growth activity commences, and can utilize currently assimilated C molecules. Another research concerning distribution and seasonal changes of carbon reserves revealed that C reserves remobilization is of minor importance for early growth of *Fagus sylvatica*, a diffuse-porous species (Barbaroux and Bréda 2002; Zein et al. 2011). Obviously, while considering the annual increment of wood in a particular growth season, both newly assimilated C and stored C are utilized, but in different proportions depending on porosity type (Palacio et al. 2011). Relative contribution of stored C was 55–70% in ring-porous species, and 35–60% in diffuse-porous species. In coniferous trees approximately 40% of stored C is used in xylem formation (Kagawa et al. 2006).

In ring-porous species, the first earlywood vessels are formed before bud break (Atkinson and Denne 1988; Frankenstein et al. 2005), whereas in diffuse-porous trees first vessels are formed when the leaves are nearly fully

developed (Lodewick 1928; Wareing 1958; Larson 1962; Aloni 1991; Schmitt et al. 2000). However, evidence suggests that timing and dynamics of vessel formation can differ between various species characterized by ring porosity (Sass-Klaassen et al. 2011). Study performed by Schmitt and colleagues (2000) on Beech tree and Black locust demonstrated several differences in their growth dynamics. Radial increment started in Black locust (a ring-porous species) one week earlier than in Beech tree (a diffuse-porous species). Bud break in Black locust occurred after radial growth initiation, while in Beech tree it occurred before initiation of wood formation. In Beech tree, radial growth dynamics was initially low; at the end of the season, after temporary increase, it decreased again. In Black locust, growth rate was maximal at the beginning of the season, and declined gradually after some time. Formation of wood ceased at the same time in both the species. Hoch and colleagues (2003) observed that among the species examined, *Quercus petraea* (ring-porous) exhibited most pronounced decrease of non-structural carbohydrate concentrations during early growth season. As discussed earlier, leaf out time in trees characterized by different wood anatomy differs significantly. A recent study based on plants growing in the northern hemisphere temperate botanical gardens (Panchen et al. 2014) has confirmed that ring-porous species leaf out later than diffuse-porous ones. Moreover, species with larger vessel diameters ($>100\mu\text{m}$) leaf out later than species with smaller vessel diameters ($\leq 100\mu\text{m}$).

Despite having certain disadvantages, wider vessels are found to be very efficient in water transport (Swaine and Grace 2007). We can conclude that wide vessels of ring-porous trees are more likely to perform better in areas with severe summer droughts, especially with high spring precipitation (at the beginning of a growth season). Some studies indicate that ring-porous trees may exhibit isohydric water status

(maintenance of steady and modest negative xylem pressure potentials during the growing season despite little rainfall) and reliance on deep soil water, as opposed to diffuse-porous species, which seem to be markedly anisohydric (developing more negative pressure potentials during drought) and probably use shallower soil water (Taneda and Sperry 2008). Considering these facts, it can be assumed that there are two different strategies for dealing with possible risks associated with embolism and cavitation among deciduous trees differing in porosity type. Ring-porous species are very susceptible to freezes (Cochard and Tyree 1990; Davis et al. 1999) that sometimes occur even in late spring. When temperature drops significantly, after these trees have developed a new conducting system, they suffer greatly from frost-induced cavitation and the following embolism (Sperry and Sullivan 1992; Sperry et al. 1994). As it seems, high vulnerability of large vessels to frost-induced cavitation makes it more favorable to postpone the moment of bud breaking and developing new leaves in order to minimize the risk of occurrence of severe dysfunction. The energetically expensive embolism repair mechanism, which is used by diffuse-porous trees, was apparently abandoned by ring-porous trees (before the start of the growing season), and thus the advantage of ring-porous trees with highly efficient earlywood vessels might be acquired in certain types of habitat. Nonetheless, both kinds of trees expend a certain amount of energy on radial growth. Each strategy is adequate for a certain environment, and each one has its drawbacks and advantages manifesting in different environmental conditions.

Vulnerability to cavitation versus plant distribution

Numerous studies have confirmed that cavitation (both drought- and freezing-induced) is one of the factors that limit geographical distribution of plants (Pockman and Sperry 2000; Martínez-

Vilalta and Pockman 2002). Range of distribution for *Larrea tridentata* (DC) Coville reflects the probable relationship between temperature responsible for total embolism and distribution limit of this species (Pockman and Sperry 1997). Sperry (1993), while studying winter embolism in *Fagus grandifolia* Ehrh., suggested that it may also affect the elevation range of the plant.

Dimensions and structural features of tracheary elements may participate in tree adaptation to varied environmental conditions. It appears that ring-porous wood has the ability to withstand low temperatures in winter, in areas characterized by the presence of dry summer and wet spring (Gizińska et al. 2013). The common occurrence of ring-porous species in the north temperate zones reflects the significance of adaptation in geographic distribution of plants (Wheeler et al. 2007). Increased vessel grouping index and more frequent occurrence of helical thickenings on the inner surface of vessels (responsible for enhancing resistance to cavitation) were reported at higher latitudes (Alves and Angyalossy-Alfonso 2000). Wheeler et al. (2007) indicated that helical thickenings of vessels are a relatively common feature of wood in Northern Hemisphere and New Zealand, and uncommon in tropical regions. Small diameter conifer tracheids, as compared to larger vessels of deciduous trees, allow conifer trees to function in low temperatures, at high latitudes, by achieving a high resistance to cavitation (Pittermann and Sperry 2003).

To some extent, plants are able to adapt to specific environmental conditions. This adaptation may be displayed in the structural differences of wood among individuals belonging to one species, which differ in the region of provenance (Martín et al. 2010; Esteban et al. 2012). Anatomical features of wood vary due to fluctuations of external factors such as water availability or temperature (Antonova and Stasova 1993, 1997; Gindl et al.

2000). These structural variations may be used in dating of processes accompanying plant growth in studies aimed at climate reconstruction (Ballesteros et al. 2010; Campelo et al. 2010). Alterations may even involve transformation into a different porosity type, as observed in *Populus euphratica* Oliv. (Liphschitz and Waisel 1970) and *Tectona grandis* L. (Nobuchi et al. 2005). However, it is obvious that there is a threshold, above which the plant is not able to adapt to unfavorable environmental conditions, and a disturbing factor (such as cavitation) becomes a limiting factor for the range of natural occurrence of species. As noted by Grace (1993), climate change, resulting in prolonged dry periods with increased temperature, may have an impact on cavitation phenomenon intensification, and thus on the functioning and survival of plants with a certain degree of tolerance.

Conclusions

In tropical rain forests radial growth may be continued throughout the year. Information available on porosity-based adaptation of trees to environmental conditions suggests that trees of tropical rain forest have sparsely distributed, very broad vessels and do not suffer from frost-induced cavitation. In temperate climate zone ring-porous trees use considerable amounts of accumulated C reserves before spring cambial activation, contrary to coniferous (non-porous) and diffuse-porous trees. As an evolutionary strategy, ring-porous wood structure has evolved from the production of completely new system of large earlywood vessels before development of new foliage in a growth season, *ipso facto* before transpiration starts. It stems from the fact, that in ring-porous trees, frost-induced embolism occurs mostly in large vessels to such a degree that it renders effective water transport virtually impossible (vulnerability to drought-induced embolism, on the contrary, seems to be independent of vessel element diameter). Non-porous and diffuse-porous trees have a quite

functional water-conducting system at their disposal when, and even before, transpiration starts (i.e. before leaf development). This is related to comparatively small size of conduits and an effective repair mechanism.

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NACZYNIOWOŚĆ DREWNA JAKO ADAPTACJA DO WARUNKÓW ŚRODOWISKA

Streszczenie

Poszczególne gatunki drzew są w różnym stopniu podatne na wystąpienie zakłóceń przepływu wody, co wiąże się ze zróżnicowaną strukturą drewna. W wyniku okresowego zamarzania wody w elementach przewodzących roślin następuje częściowa utrata przewodności hydraulicznej. Drzewa pierścieniowonaczyniowe i rozpierchłonaczyniowe wykształciły odmienne mechanizmy pozwalające na uzyskanie odpowiedniej funkcjonalności na początku sezonu wegetacyjnego. Wiążą się one z produkcją nowych naczyń, o dużych wymiarach i wysokiej przewodności w przypadku drzew pierścieniowonaczyniowych, a u drzew rozpierchłonaczyniowych z ponownym napełnianiem wodą niefunkcjonujących, zembolizowanych naczyń. Obie strategie związane są z odmiennym sposobem korzystania ze zgromadzonych rezerw węglowych.