Chapter 2
The Hydraulic Architecture of Conifers

Uwe G. Hacke, Barbara Lachenbruch, Jarmila Pittermann, Stefan Mayr, Jean-Christophe Domec, and Paul J. Schulte

1 Introduction

Conifers survive in diverse and sometimes extreme environments (Fig. 2.1a–f). Piñon-juniper communities are found in semi-arid environments, receiving ca. 400 mm of yearly precipitation (Linton et al. 1998), which is less than half the

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U.G. Hacke (✉)
Department of Renewable Resources, University of Alberta,
442 Earth Sciences Building, Edmonton, AB, Canada, T6G 2E3
e-mail: uwe.hacke@ualberta.ca

B. Lachenbruch
Department of Wood Science and Engineering, Oregon State University,
Corvallis, OR 97331, USA

Department of Forest Ecosystems & Society, Oregon State University, Corvallis, OR USA
e-mail: barb.lachenbruch@oregonstate.edu

J. Pittermann
Department of Ecology and Evolutionary Biology, University of California,
Santa Cruz, CA 95064, USA
e-mail: jpitterm@ucsc.edu

S. Mayr
Department of Botany, University of Innsbruck, Sternwartestr. 15, Innsbruck 6020, Austria
e-mail: stefan.mayr@uibk.ac.at

J.-C. Domec
Bordeaux Sciences Agro—INRA, UMR ISPA,
1 cours du Général de Gaulle, Gradignan 33175, France

Nicholas School of the Environment, Duke University, Durham, NC 27708, USA
e-mail: jc.domec@agro-bordeaux.fr

P.J. Schulte
School of Life Sciences, University of Nevada, Las Vegas, NV 89154-4004, USA
e-mail: paul.schulte@unlv.edu

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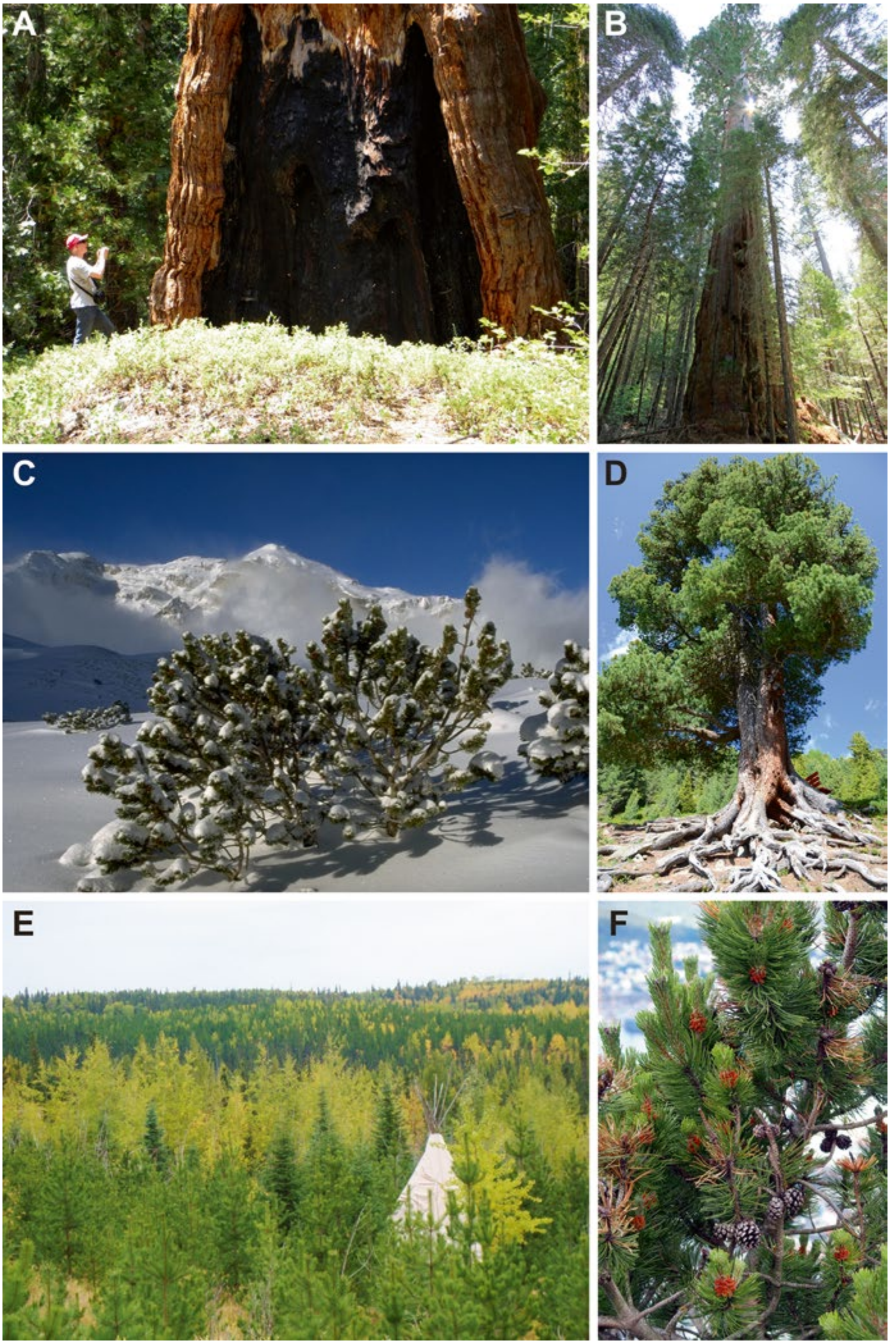

Fig. 2.1 Conifers growing in diverse habitats. (**a**, **b**) *Sequoiadendron giganteum* in the Sierra Nevada mountains of California (photos: B. Pratt). (**c**) *Pinus mugo*, partly covered by snow, at the timberline in Tyrol, Austria (photo: S. Mayr). (**d**) *Pinus cembra* at the alpine timberline in Tyrol, Austria (photo: S. Mayr). (**e**) Boreal mixedwood forest near Whitecourt, Alberta (photo: A. Schoonmaker). The teepee was constructed for a shading experiment. (**f**) *Pinus sylvestris* near Bergen, Norway (photo: A. Jacobsen)

average precipitations received by other coniferous tree species worldwide. *Picea mariana* and *Larix laricina* grow in boreal peatlands where they face fluctuating water tables and cold, often frozen soils (Lieffers and Rothwell 1987). Timberline trees such as *Pinus cembra* experience short growing seasons and cope with frost, winter desiccation, and mechanical challenges (Mayr et al. 2012) (Fig. 2.1c, d). The Cupressaceae family is particularly diverse in terms of the morphology and habitat preference exhibited by its members (Pittermann et al. 2012). While *Taxodium distichum* is adapted to water-logged soils, many *Juniperus* and *Pinus* species are exceptionally drought tolerant. Conifers are "archetypical stress tolerators" (Brodribb et al. 2012), and their xylem structure plays a key role in enabling them to survive in stressful habitats. However, north temperate conifers can also occupy more favorable environments; for example, conifers are an integral component of North American mixed eastern deciduous forests, and the Pacific Northwest landscape is characterized by Douglas-fir and old-growth conifer forests.

The water-conducting cells in the xylem of conifers are tracheids, which are overlapping single-celled hollow conduits, closed at both ends. Water moves through a tracheid's lumen, then passes through a pit pair into the lumen of an adjacent tracheid. Relative to vessel-based xylem of the vast majority of angiosperms, the conifers' ancestral vascular system has been regarded as an Achilles heel that limits the conifers' physiological capacity for growth and competition (Bond 1989; Brodribb et al. 2012). This is understandable: vessels are comprised of stacked, single-celled vessel elements that can be wider than tracheids, such that maximum hydraulic efficiency of angiosperm xylem can be one to two orders of magnitude higher than that of conifers (Ewers 1985). However, when observed through the lens of natural history, conifer xylem could hardly be called a handicap. Indeed, the tracheid-based xylem structure of conifers supports the largest (*Sequoiadendron giganteum*, *Pseudotsuga menziesii*) and tallest (*Sequoia sempervirens*) trees (Fig. 2.1a, b). Bristlecone pine (*Pinus longaeva*) trees are among the oldest known living eukaryotic organisms; several specimens still alive are well over 4,000 years of age (Flanary and Kletetschka 2005).

In this chapter, our goal is to provide a synthesis of what we currently know about the hydraulic architecture of conifers. In the last decade or so, much has been learned about the ecophysiological processes in conifer taxa and how they relate to xylem properties. In future years, we will likely expand our knowledge of topics such as needle and fine root hydraulics, aquaporin function, and phloem transport. While *Arabidopsis thaliana* and other herbaceous species will continue to be widely used as model systems in molecular and developmental biology, it is clear that tall, long-lived woody plants face unique challenges in terms of water and assimilate transport, biomechanics, storage, reproduction, and stress tolerance.

We start with information on how the xylem functions in stems, coarse roots, and then briefly, in needles. The focus is on the structural means by which xylem transports water in conditions with plentiful water, drought, and freezing (Sect. 2). The ecophysiology of a woody plant, however, results from the interaction of the whole plant with the environment, as well as its growth and repair abilities. We therefore review information on within-plant variation in xylem hydraulic properties and link some of the relationships of hydraulic properties to a plant's physiological capabilities (Sect. 3).

2 Conifer Xylem and How It Works

2.1 Tracheids: The Conduits for Water Transport

While fiber tracheids and libriform fibers provide structural support in angiosperm xylem, conifer xylem lacks fibers so the tracheids must play a dual role in both transporting water to the canopy, and physically supporting it. More than 90 % of a conifer xylem cross section consists of tracheids (Fig. 2.2a, b). Schulte (2012b) estimated that there is a total number of ~500 million tracheids in the trunks of young Douglas-fir trees. In terms of cell types, conifer wood may therefore appear simple in structure. Closer inspection, however, reveals much variation in cell dimensions, wall thickness, pit structure, and other structural features within a cross section, as well as variation in the ultrastructure of the cell wall itself. Depending on developmental constraints and according to hydraulic and biomechanical tasks, the morphology of tracheids varies considerably, and this variation has direct implications for transport safety and efficiency.

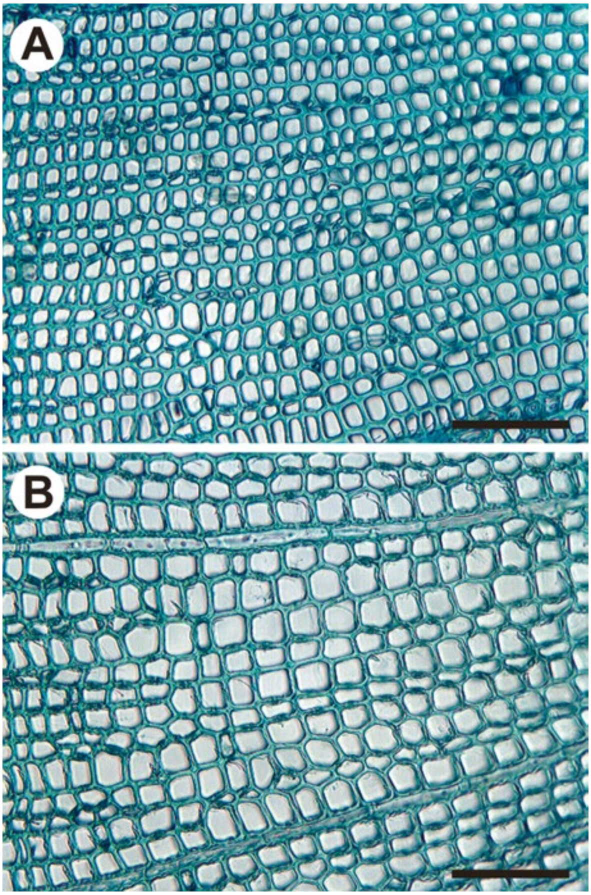

Fig. 2.2 Cross sections showing branch xylem of *Widdringtonia cedarbergensis* (**a**) and *Taxodium mucronatum* (**b**). *W. cedarbergensis* is a xeric species. Its xylem is extremely resistant to cavitation and is characterized by narrow, thick-walled tracheids. *T. mucronatum*, by contrast, is primarily a riparian tree. Tracheids are wider and less reinforced than those of *W. cedarbergensis*. Scale bars = 100 μm. Photos: J. Pittermann

2.1.1 Tracheids and Xylem Structure

Tracheid diameters usually vary between 5 and 80 µm (Tyree et al. 1994; Linton et al. 1998; Pittermann and Sperry 2003; Wilson and Knoll 2010, their Table 1; Schulte 2012b; McCulloh et al. 2014). Diameters tend to be smaller in twigs than in trunks and roots (Bannan 1965; Dunham et al. 2007; Domec et al. 2009). Tracheid diameter is limited by at least two factors. Their tangential expansion during development is likely limited by the width of fusiform initials. Tracheids are formed side by side tangentially. Developing vessel elements, by contrast, can expand at the expense of adjacent fibers and axial parenchyma cells. An indirect limit on tracheid diameter relates to the fact that tracheids, being unicellular, are limited in length. If conduits cannot increase in length as they increase in diameter, their hydraulic conductivity (for a definition of hydraulic conductivity see Tyree and Ewers 1991) will eventually stop increasing (Sperry et al. 2006). For a maximum tracheid length of 5 mm, the model of Hacke et al. (2004) predicted no further increase in tracheid conductivity for an increase in diameter beyond approximately 70–80 µm, which is also close to the observed limit of tracheid diameters.

Tracheid length is usually less than 5 mm (Bannan 1965; Sperry et al. 2006; Dunham et al. 2007; Domec et al. 2008; Schulte 2012b). Longer tracheids are associated with wood that has both higher hydraulic efficiency and higher mechanical properties such as bending strength (Rundel and Stecker 1977; Domec and Gartner 2002a; Rosner 2013), but the relationship with mechanical properties is driven by differences in cell wall properties that are usually associated with cells in positions where cells are longer, and not related to cell length per se (Lachenbruch et al. 2011).

Tracheid length may reflect the length of the fusiform initials in the cambium, but that is unclear. In a typical angiosperm or gymnosperm, xylem cell lengths increase asymptotically along a transect outward from the pith (Panshin and Zeeuw 1980). This relationship, however, is not seen in several circumstances (e.g., roots of *Pseudotsuga menziesii*, Peterson et al. 2007), suggesting that the length of cambial initials does not have total control over tracheid length. The relatively short and narrow tracheids found in extant conifers contrast with the tracheids belonging to *Medullosa*, an extinct, Carboniferous seed fern with a putatively upright habit, similar to modern tree ferns (Taylor et al. 2009). Medullosan tracheids measured up to 28 mm in length and commonly exceeded 150 µm in diameter (Wilson et al. 2008; Wilson and Knoll 2010). These enormous tracheids in the extinct seed fern suggest that short, narrow tracheids in stems of extant gymnosperms are not merely a reflection of developmental constraints, but that tracheid dimensions are under selection for both hydraulic and structural performance. Indeed, the stem tracheids of the late-Devonian pro-gymnosperm *Archaeopteris* bear this out. Fossils show this spore-bearing tree to be a hybrid of conifer and fern attributes whereby the trunk exhibits conifer like, pycnoxylic xylem that supports a canopy of fern-like leaves (see Chap. 1). As in extant conifers, stem tracheids are on average narrower than 30 µm, thereby reflecting the support function, whilst root tracheids frequently reach diameters in excess of 40 µm (Domec et al. 2009, Pittermann, unpublished data). Interestingly, tracheids in fern primary xylem can also be much longer and wider than tracheids of conifers (see Chap. 1), which is presumably possible because fern tracheids play little role in mechanical support of the plant.

As stated above, a volume of coniferous wood is typically about 90–93 % tracheids (Panshin and Zeeuw 1980); the remaining 7–10 % is parenchyma. In contrast to the tracheids, most parenchyma cells maintain their nuclei and cytoplasm until the cells die, at heartwood formation. A characteristic feature of conifer wood is the relatively small amount of parenchyma, particularly axial parenchyma (Evert 2006), compared to the angiosperms, which can have well over 50 % of their xylem volume as parenchyma (although 10–40 % is more typical for commercial temperate-zone hardwoods, Panshin and Zeeuw 1980). The exact function of axial and ray parenchyma is not entirely understood, but they certainly have roles in the transport of chemical signals and other constituents and may contribute to the reversal of embolisms, heartwood formation (Dellus et al. 1997; Taylor et al. 2002; Spicer 2005), and both inducible and constitutive defense. In-depth information can be found in Chap. 8. Xylem parenchyma has three forms in coniferous wood: axial parenchyma, radial (ray) parenchyma, and, in some species, epithelial cells (the cells surrounding resin canals that produce the resin that helps plants defend against biotic agents after injury). We have only rudimentary understanding of the three-dimensional configuration of the parenchyma cells network; in fact, LaPasha and Wheeler (1990) report the unexpected finding that the epithelial cells do not appear to have symplastic connections between the radial and the axially oriented resin canals. Ray parenchyma is in contact with phloem tissue (Fig. 2.3a, b) and thus provides a means by which materials in the phloem can move into the xylem and vice versa. Aquaporin water channels are expressed in ray parenchyma cells (Fig. 2.3a–c), which may facilitate water exchange between ray cells and between rays and axial tracheids. Curiously, only a subset of the conifer species have normal resin canals (those not formed by trauma), and most of these species also have a feature called a ray tracheid, which is a dead cell within the ray that somewhat resembles an axial tracheid in that it has bordered pits, but that has not been shown to transport water (Barnard et al. 2013).

2.1.2 Tracheids and Specific Conductivity

The longer conduits are for a given diameter, the farther apart the end walls are and the less they contribute to the total flow resistance. Examining root and stem wood from 19 conifer species belonging to the Pinaceae, Cupressaceae, Podocarpaceae, and Araucariaceae, Pittermann et al. (2006a) found that total tracheid resistivity was nearly equally divided between lumen and pit, with the passage through the pits contributing approximately 64 % to the total tracheid resistivity. Remarkably, the limitation to hydraulic efficiency caused by passage through the pits was independent of tracheid size in the conifers surveyed. This was associated with proportionality between tracheid diameter and length. The observed tracheid diameter versus length allometry appeared to optimize hydraulic efficiency (Pittermann et al. 2006a).

Mean conduit diameters usually vary significantly between conifer stems and conifer roots, and between conifer stems and angiosperm stems (Fig. 2.4a). Samples were typically 8–12 mm in diameter and mostly represented juvenile xylem. Conifer

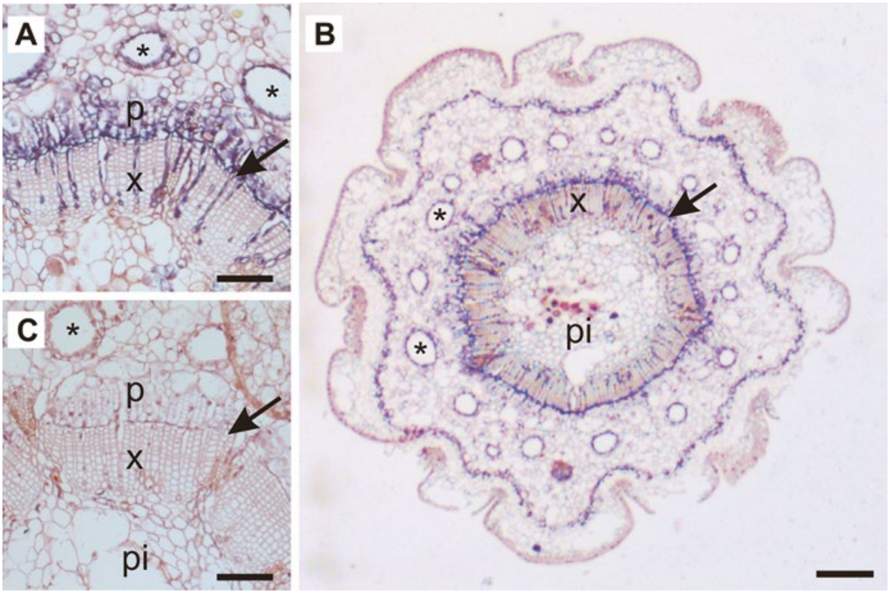

Fig. 2.3 In situ mRNA hybridization of the aquaporin gene *PgPIP1;2* in cross sections of a white spruce (*Picea glauca*) twig. Sections were hybridized with DIG-labeled antisense *PgPIP1;2* RNA probes (**a**, **b**) as described previously (Laur and Hacke 2014). A negative control hybridized with DIG-labeled sense probe is shown in (**c**). Regions of aquaporin expression are indicated by *dark purple* staining. The gene was expressed in xylem rays, the cambial region (*arrows*), the phloem, and in other cortex cells. No staining was found in the negative control. *p* phloem, *pi* pith, *x* xylem. *Asterisks* mark resin ducts. *Bars* in (**a**) and (**c**) = 100 µm, *bar* in (**b**) = 200 µm. Photos: J. Laur

species were from Pinaceae, Cupressaceae, Podocarpaceae, and Araucariaceae. The angiosperm species were eudicot shrubs, trees, and vines from numerous North American habitats and taxa. Conifer stems (mostly branches) had by far the narrowest conduit diameter range. While the median conduit diameter of angiosperm stems and conifer roots was similar, some ring-porous trees and vines had conduits that were much wider than those of conifers (note the log-scale).

Differences in conduit diameter have consequences for transport efficiency, and xylem efficiency in return impacts water supply to the leaf and stomatal conductance (Pittermann et al. 2012). In the data set shown in Fig. 2.4b, vines and some conifer roots exhibited the highest xylem area-specific conductivities. Remarkably, the median xylem area-specific conductivity at full saturation (K_{smax}) of conifer roots was higher than in the other groups. This is explicable in the light of highly conductive pits and the fact that a large fraction of conifer wood is occupied by conduits owing to the double role of tracheids in transport and mechanical support (Sperry et al. 2012). For a given mean conduit diameter, conifer xylem has slightly higher conductivities than angiosperm xylem in which vessels are dispersed in a fiber-parenchyma matrix (Sperry et al. 2006, their Fig. 3B).

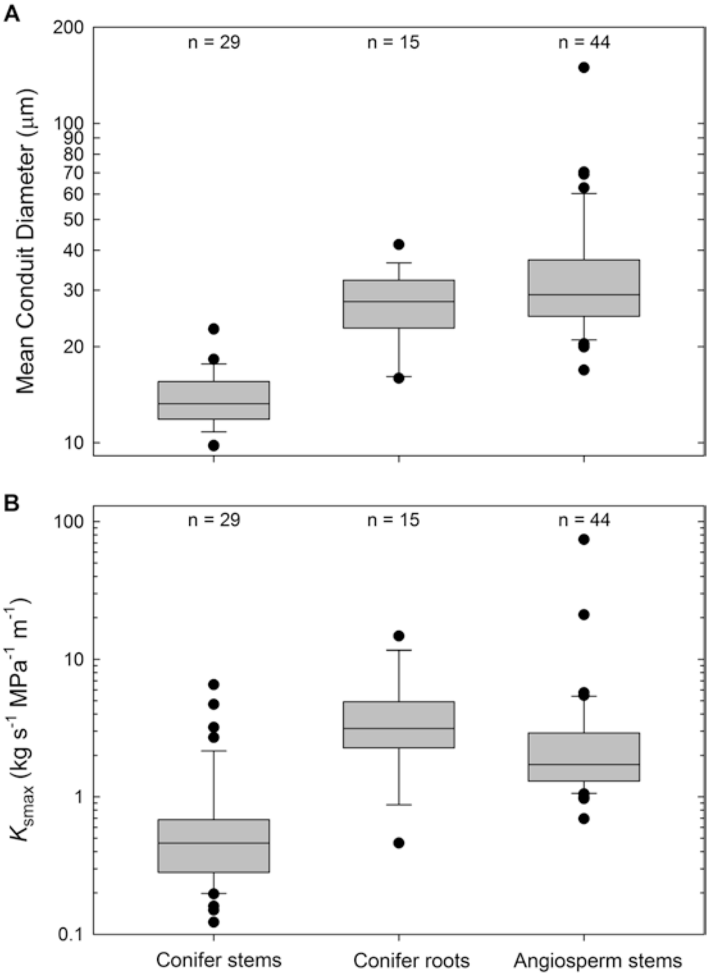

Fig. 2.4 (**a**) Box plots of mean conduit diameters and (**b**) xylem area-specific conductivity (K_{smax}) of conifer stems, conifer roots, and angiosperm stems. The ends of the boxes define the 25th and 75th percentiles. The *middle line* in the boxes represents the median. The error bars (*whiskers*) define the 10th and 90th percentiles. Outliers beyond the whiskers are individually plotted as *circles*. The data is for flushed samples that were at least 14 cm in length, and was taken from various publications (Hacke et al. 2006; Pittermann et al. 2006a; Hacke and Jansen 2009; Schoonmaker et al. 2010; Schreiber et al. 2011)

However, vessels can achieve greater maximum diameters than tracheids, which can ultimately provide greater conductivity per xylem area. Tropical trees reach the greatest maximum transport per stem cross-sectional area since they can combine large vessels with large sapwood areas (Sperry et al. 2012). Nonetheless, in habitats where vessel diameter is constrained by freezing and/or drought stress, both xylem types should exhibit similar K_{smax} values, and this may help conifers compete with angiosperms (Pittermann et al. 2005; Sperry et al. 2008).

2.2 *Bordered Pits: The Tracheid-to-Tracheid Valves for Water Transport*

Because water transport relies on the movement of water under tension (negative hydrostatic pressure), the introduction of gas would result in a breakage of the water column. Therefore, there must be very strong selective pressure for avoiding the breakage of the water column by gas in the tissues (e.g., earlywood) through which transport is needed. Coniferous pits are elegant structures that permit water movement from one cell to another, whilst protecting the cells from air entry in case an adjacent tracheid is gas-filled (see below). Coniferous bordered pits are circular perforations in the tracheid cell wall, paired with a coincident perforation on the adjacent tracheid (and so technically, they are considered as pit pairs). The volume between the two borders is called the pit chamber. The perforation is covered with a torus–margo pit membrane (Fig. 2.5a–d). The number of bordered pits within one earlywood tracheid can vary from approximately 15 to >100 (Evert 2006; Schoonmaker et al. 2010; Schulte 2012b). Pit pairs are largely confined to the radial walls, suggesting a relative ease of water-sharing in the tangential direction around a stem, as opposed to the radial (between growth rings) direction. Pit pairs are most abundant near the tips of the tracheids, which appears to limit the loss of flow resistance across the entire cell (Aumann and Ford 2002). While narrow tracheids have only one row of inter-tracheid pits, wide tracheids (e.g., in roots) often have two rows of pits. Two pit rows may connect a tracheid with two distinct tracheids or just one adjacent conduit (Schulte 2012b). Details of how pits are formed are provided in Chap. 3. The structure and function of these pits represents a unique compromise between requirements for efficient water transport and the need to prevent spread of air from embolized tracheids (Pittermann et al. 2005; Domec et al. 2008). Since tracheid length is limited, pit characteristics are a major determinant of tracheid and whole xylem hydraulic conductivity.

In the center of the pit membrane is a thickened, approximately circular torus, which is impermeable to water. The torus is surrounded by a porous membrane region called the margo, which provides passage for water. When two adjacent tracheids are water-filled, the torus is centrally located in the pit chamber (Fig. 2.6a), allowing water flow between tracheids through the pores of the margo, as influenced by passive movement according to the pressure gradients. Should an air bubble enter one of the tracheids, the membrane will move according to the pressure gradient, such that the torus will block the aperture in the pit border (Fig. 2.6b). This state is called pit aspiration.

Across species and plant organs (roots and stems), pit membrane diameter scaled linearly with both torus and aperture diameters (Fig. 2.7). In Pinaceae species, the torus represented 45–49 % of the pit diameter (Hacke et al. 2004; Domec et al. 2006; Hacke and Jansen 2009). In tall trees, this ratio may vary with height. The tight scaling of pit dimensions is likely to have important functional implications. Conifers have circular bordered pits, and the valve, consisting of the torus and margo, works well to seal such pits. Angiosperms, in contrast, have a much wider range of pit shapes, including the extreme, the scalariform pit, which is relatively

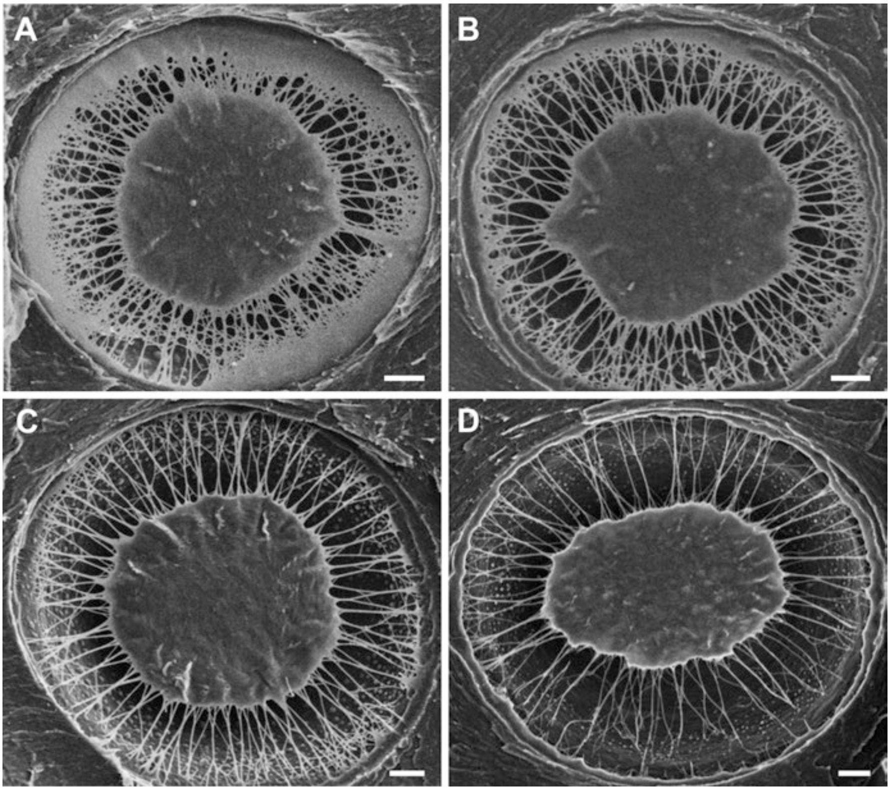

Fig. 2.5 Scanning electron microscopy images showing torus–margo pits of lodgepole pine (*Pinus contorta*) stems. Samples were taken from open-grown (**a**–**c**) and shaded (**d**) trees as explained in Schoonmaker et al. (2010). The images represent a continuum of margo porosities. Some pits have a dense margo with small pores, particularly near the edge of the membrane (**a**) while other pits have few margo "spokes" and large pores between the margo fibrils. The latter was particularly frequent in shaded trees (**d**). *Bars* = 1 μm. Images: A. Schoonmaker and G. Braybrook

long and narrow. Although there are tori or pseudotori in some angiosperm species (for details, see Chap. 3), these pits lack the highly conductive margo portion and are not at all like those of conifers in conductive ability (Carlquist 2012).

In many cases, the pit membrane can rebound from an aspirated position. This capacity is a prerequisite for the recovery of hydraulic conductivity after embolized tracheids have been refilled. In *Picea abies*, very close agreement has been found between the amount of winter embolism (expressed as percent loss of hydraulic conductivity, PLC) and the ratio of aspirated versus open pits (Mayr et al. 2014). Nearly one-half of all inter-tracheid pits were closed in January and opened as PLC decreased and conductivity was reestablished in spring.

The valve action of torus–margo pits also appears to facilitate embolism repair when the transpiration stream is under tension (Mayr et al. 2014). Under these conditions, refilling in individual tracheids may only be possible if these conduits are

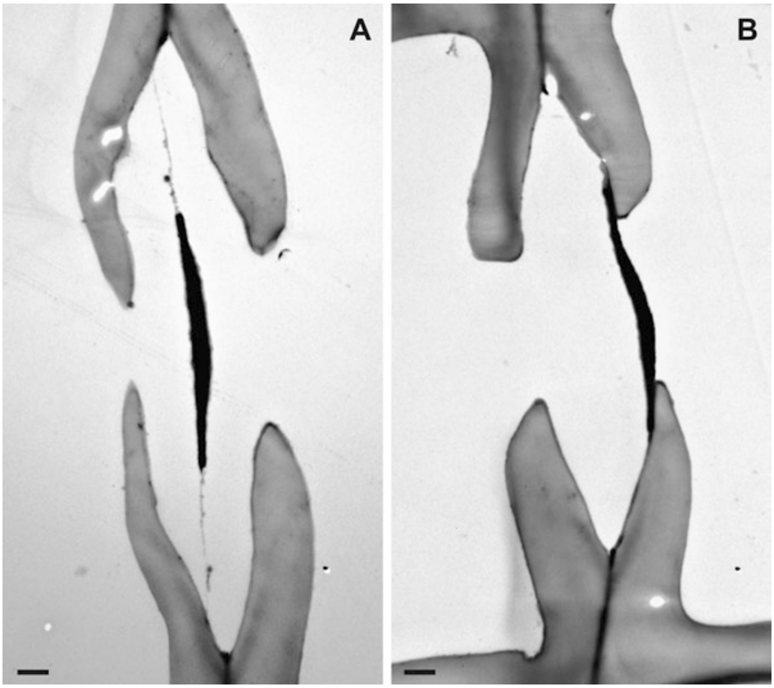

Fig. 2.6 Transmission electron micrographs of pit membranes in roots of *Picea glauca*. The membrane is relaxed (**a**) or aspirated, blocking the aperture (**b**). *Bars* = 1 μm. From Hacke and Jansen (2009)

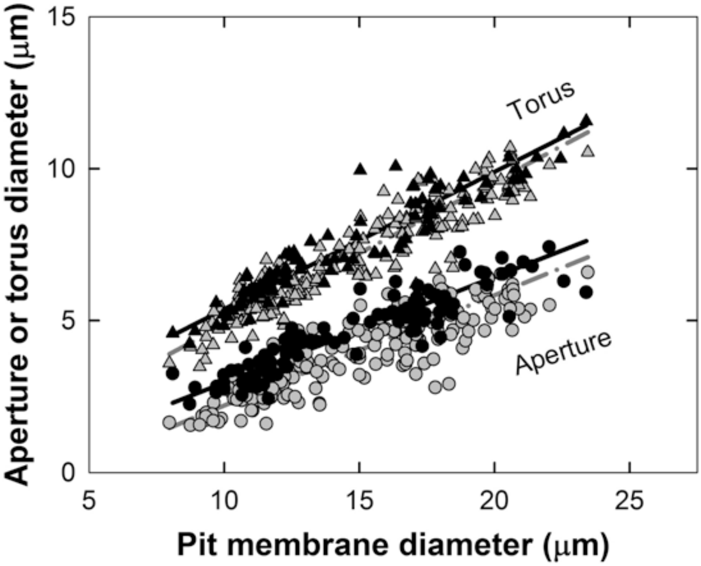

Fig. 2.7 Torus (*triangles*) or pit aperture (*circles*) diameter versus pit membrane diameter for root and stem tracheids. Measurements were either done on surface views of pits (*closed symbols* and *solid lines*) or on cross sections of pits (*gray symbols* and *dashed lines*) as explained previously (Hacke and Jansen 2009). The regression lines are shown for pooled stem and root data. The data were taken from three boreal conifer species (*Abies balsamea*, *Picea glauca*, and *Picea mariana*). From Hacke and Jansen (2009)

hydraulically isolated from the transpiration stream (Zwieniecki and Holbrook 2009). Otherwise, any drop of water exuded into a refilling conduit would immediately be pulled out by surrounding water columns under tension (Holbrook and Zwieniecki 1999). Conifer pits efficiently seal off empty from functional tracheids as long as the pressure difference across pits is lower than the cavitation threshold (see Sect. 2.2.1). This mechanism will isolate tracheids during refilling and dissolution of entrapped gas in the growing water films. When refilling of a tracheid is completed, the equilibration of the tracheid's water potential with surrounding water columns may then cause all pits to open simultaneously.

2.2.1 Pit Structure and Vulnerability to "Air-Seeding"

While the valve action of a bordered pit pair creates a seal that prevents the spread of gas from an embolized tracheid to the functional, water-filled tracheids, the seal will fail when the pressure difference across the pit membrane exceeds the "air-seed pressure," at which air leaks past and nucleates cavitation in the adjacent tracheid (Hacke et al. 2004, their Fig. 1C; Domec et al. 2008). Available evidence suggests that beyond this air-seed pressure, failure of the valve occurs when the torus is displaced from its sealing position, exposing pores in the margo through which gas enters the water-filled tracheid (Sperry and Tyree 1990; Domec et al. 2006). How can differences in cavitation resistance between species and plant organs be explained in the light of pit structure?

Based on the sealing function of the torus, we expect that the size of the torus relative to the pit aperture impacts cavitation resistance. A torus too small for a given aperture diameter may result in greater vulnerability to air-seeding. A torus wider than the optimum reduces margo area and conductivity. One may therefore hypothesize that there is an optimal range of "torus overlap." The term torus overlap may be defined as the fraction of the pit border that is covered by the torus $[(D_t - D_a)/(D_m - D_a)]$, where D_t, D_a, and D_m are torus, aperture, and pit membrane diameter, respectively. Reported values of torus overlap are between 0.21 and 0.38 (Hacke et al. 2004; Hacke and Jansen 2009).

Torus overlap can also be quantified by using the D_t/D_a ratio (Domec et al. 2008). When D_t and D_a were measured in Douglas-fir trees along a height gradient of 85 m, striking trends were found. While D_t remained relatively unchanged (Fig. 2.8a), D_a decreased significantly with increasing height (Fig. 2.8b). As a result, there was an increase in the D_t/D_a ratio with increasing height in both trunk and branch tracheids (Fig. 2.8c). Higher D_t/D_a ratios mean that the pit can sustain a greater pressure difference between an embolized and a water-filled tracheid (ΔP); however, smaller aperture diameters come at the expense of a decline in hydraulic conductivity (Domec et al. 2008).

In 15 species of Cupressaceae, the D_t/D_a ratio also showed a strong relationship with cavitation resistance (expressed as the xylem pressure inducing 50 % loss of hydraulic conductivity, P_{50}). The D_t/D_a ratio was mainly determined by variation in D_a, which decreased nearly twofold with more negative cavitation pressures

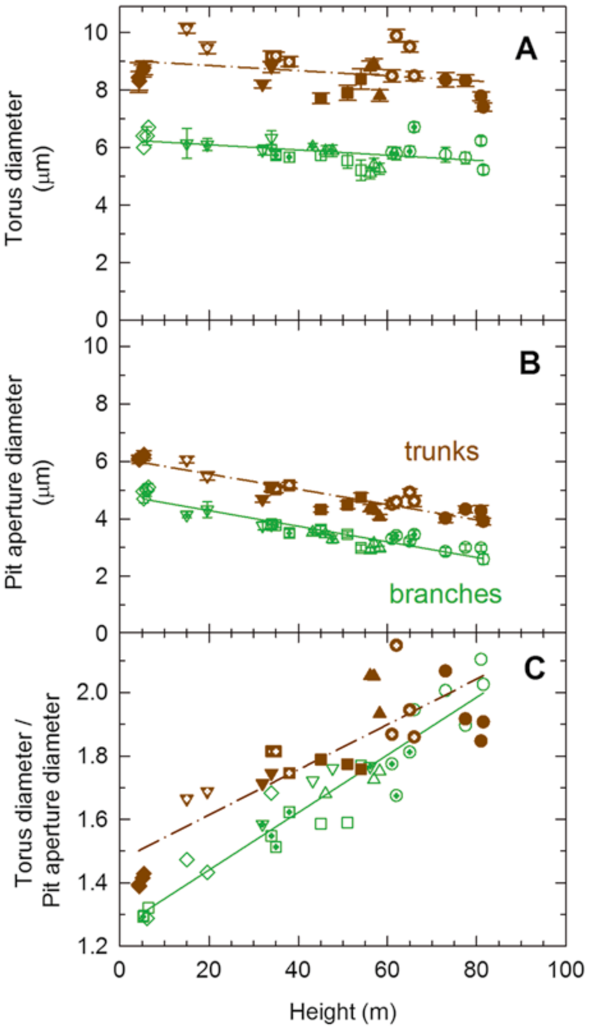

Fig. 2.8 Pit anatomical traits as a function of height in branches (*green*) and trunks (*brown*) of large Douglas-fir trees. While torus diameter (**a**) remained relatively constant with height, pit aperture diameter (**b**) decreased significantly. As a result, the ratio of torus to aperture diameter (**c**) increased with height. Values are means ± 1 standard deviation. From Domec et al. (2008)

(Pittermann et al. 2010). Lower D_a was also observed at higher elevation in *Picea abies*, which is exposed to increasing frost near the timberline (Mayr et al. 2002). Finally, a recent survey reported that torus overlap increased with increasing cavitation resistance (Bouche et al. 2014). Available data from Pinaceae and Cupressaceae therefore indicate that torus overlap is a key determinant of cavitation resistance, and that it is largely driven by variation in D_a.

Aside from torus overlap, cavitation resistance is potentially impacted by a wide variety of other structural pit features. To name a few, torus extensions, torus thickness/flexibility, the presence of pores in the torus, margo properties, the distance the margo must stretch to reach the aperture, and the surface properties of the torus and the internal side of the pit border (smooth or rough surface) have all been implicated

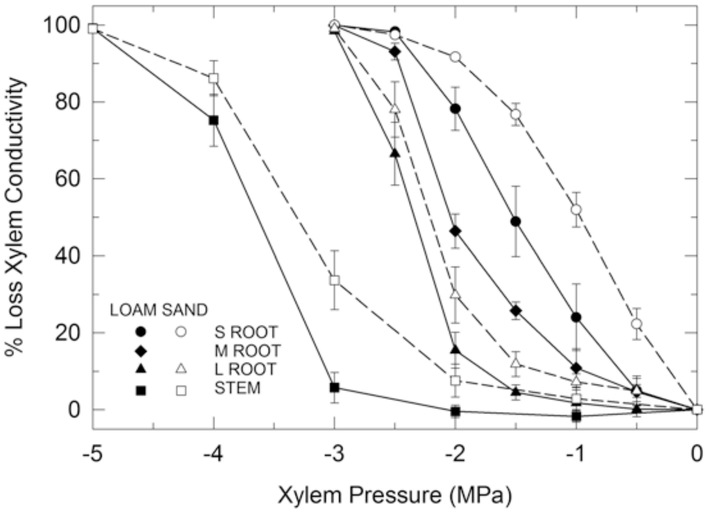

Fig. 2.9 Vulnerability curves showing the percentage loss of hydraulic conductivity as a function of xylem pressure for roots (*S* small 1.6–4.1 mm diameter; *M* medium 4.2–6.4 mm diameter; *L* large 8.2–13 mm diameter) and stems of *Pinus taeda* trees growing in sand (*open symbols*, *dashed lines*) versus loam (*solid symbols* and *line*) soil. Means and standard errors are shown for segments from six trees per site. From Hacke et al. (2000)

in potentially affecting air-seeding (Hacke et al. 2004; Cochard et al. 2009; Hacke and Jansen 2009; Delzon et al. 2010; Schoonmaker et al. 2010; Jansen et al. 2012; Bouche et al. 2014; Plavcová et al. 2013). However, some reports are contradictory (e.g., regarding torus thickness and torus extensions), and it is not always clear whether observed correlations reflect causal relationships. Nonetheless, neither torus extensions nor punctured tori appear to be rare phenomena across Pinaceae species, and it has been hypothesized that such “irregularities” in pit structure can have substantial influence on cavitation resistance (Plavcová et al. 2013). While punctured tori appear to be associated with increased vulnerability to cavitation (Jansen et al. 2012), the impact of torus extensions on ΔP may be species-specific (Pittermann et al. 2010; Schoonmaker et al. 2010).

The xylem of conifer stems typically shows sigmoidal vulnerability curves with a well-defined and highly reproducible cavitation threshold (Fig. 2.9). This may in part be explained by the fact that earlywood tracheids, which contribute to most of the water flow within a ring (Domec and Gartner 2002b) are relatively uniform in terms of size and hydraulic properties compared with a typical population of vessels in an angiosperm stem. Assuming that cavitation resistance is to a large extent determined by pit structure, one may conclude that pit structure in earlywood tracheids is also fairly homogeneous, at least in terms of the structural features of pits that relate to ΔP. This conclusion is consistent with the tight scaling of D_m, D_t, and D_a (Fig. 2.7), but it seems inconsistent with the astonishing variability in margo porosity (Fig. 2.5a–d) and the seemingly random occurrence of features like torus extensions and torus pores that can be observed even within an axis. This could either mean that these features have only minor impact on cavitation resistance or it may be an indication that cavitation resistance is not as much determined by torus and margo structure as previously thought. Cavitation is therefore probably not a direct consequence of the rupture of the margo strands or when air is sucked through the margo pores, but rather related to the capacity of the torus to stay in place when aspirated. These minute mechanical pit features may contribute to the stochasticity of the cavitation response in conifers, and probably reflect some degree of variation associated with wall digestion during tracheid development. The available evidence indicates that selection has favored adjustments in torus thickness, torus diameter, and aperture diameter in a predictable direction that balances cavitation resistance with efficient water flow.

In latewood tracheids, air seeding appears to occur through margo pores without torus aspiration (Domec and Gartner 2002b). Latewood is highly vulnerable to cavitation at normal operating pressures, and may serve more in water storage than in transport (Domec and Gartner 2002b; McCulloh et al. 2014). Similarly, compression wood, which has mainly mechanical function, also showed higher vulnerability to drought-induced cavitation compared to opposite wood (Mayr and Cochard 2003).

2.2.2 Pit Structure and Hydraulic Conductivity

Many conifer trees attain impressive heights (Fig. 2.1b), despite the fact that tracheids are only a few mm in length. Water would have to flow past a minimum of 7,500 pit pairs to get to the top of a 30 m tall tree if tracheids average 4 mm long and water flowed from the tip of one tracheid into the base of the next. Such flow is possible because torus–margo pits are very efficient in terms of water transport (Hacke et al. 2004; Pittermann et al. 2005, 2006a; Sperry et al. 2006; Domec et al. 2008). What is it that makes these pits so efficient? As noted previously (and apparent in Fig. 2.5), the conifer (torus–margo) membrane has much larger pores than does the typical membrane in angiosperms (Pittermann et al. 2005; Choat et al. 2008; Choat and Pittermann 2009). This porous nature of conifer pit membranes was suggested a century ago in drawings by Bailey (1913). Estimates of the resistivity of the margo in conifers fall within a range of 3- to 40-fold lower than found for the pit membrane of angiosperms (Hacke et al. 2004). Choat et al. (2008) reviewed a large number of angiosperm and conifer estimates, also showing a clear distinction in pit membrane resistivity between conifers and angiosperms despite considerable variation.

Modeling studies of flow through conifer pits using a computational fluid dynamics approach (Lancashire and Ennos 2002; Schulte 2012a) can help to distinguish resistance components attributed to various pit structures such as the pit aperture, and the two components of the membrane: the torus providing an obstruction to flow across the pit membrane and the margo. In a study of pits in *Picea mariana* (Schulte 2012a), the margo contributed the majority of the resistance in the modeled pit from a sun-grown tree (63 % of pit resistance). But in the shade-grown case, the margo contributed only 38 % of the total pit resistance. The differences appeared to be due to the presence of wider pores in the shade pit, suggesting that considerable variation in the pit membrane component of resistance is likely to occur among

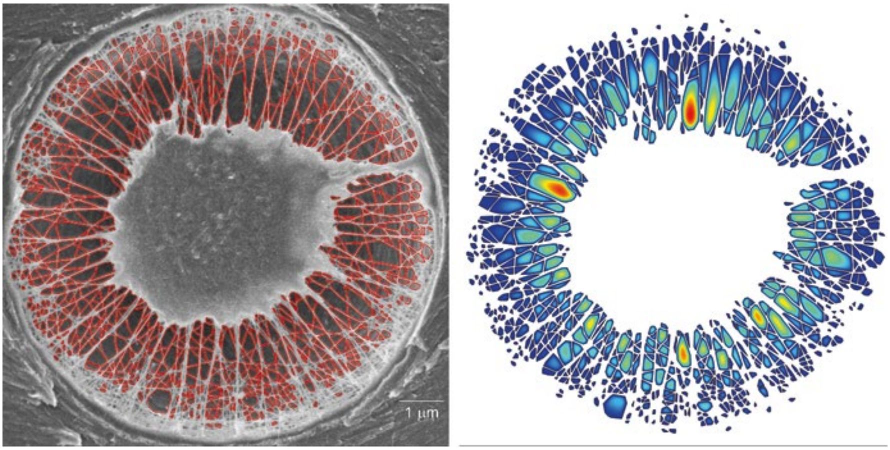

Fig. 2.10 Modeling of pits in *Picea mariana* stems. The *left* image shows an SEM view of a pit membrane (torus and margo) where the pore edges have been drawn as polygons in AutoCAD for import into the fluid dynamics model. The *right* image shows results from the model solution, whereby the color scale (0–7 mm/s as *red*) shows flow velocity within the margo pores. See Schulte (2012a) for details

conifers. Model solutions can be used to estimate the flow rate through individual pores (Fig. 2.10) and the total contribution to flow of each margo pore. Although the wide pores are much fewer in number than narrow pores, they are more significant for flow: for the pits modeled, only a few percent of the margo pores accounted for nearly half of the total flow. As shown in Fig. 2.5a, b, there is a tendency for denser margo structures at the edge of the membrane. Pores tend to be larger closer to the torus, and this has implications for hydraulic conductivity. A characteristic of flow through the margo pores (apparent in Fig. 2.10) is that flow tends to be greater through pores at the inner edge of the margo adjacent to the torus. This suggests that margo structure (the distribution of margo strands and pore size) might be somewhat optimized for providing high flow rate while also providing strength for mechanical support of the torus.

Most of the work described above has been done on Pinaceae and Cupressaceae species. However, not all conifers may demonstrate the functionality and selective directionality of pit attributes that have been found in the north temperate conifers (Pittermann et al. 2006a).

2.3 *Freezing-Induced Embolism*

Wide tracheids, such as those found in the riparian bald-cypress, *Taxodium distichum* commit species to environments without freezing or water stress. Conduit diameter determines vulnerability to freezing-induced embolism; conifers with narrow tracheids are better protected against freezing-induced embolism in cold climates than trees with wider conduits (Pittermann and Sperry 2003). Indeed, boreal latitudes, north-temperate treelines and high deserts such as those in the south-western USA are dominated by members of the Pinaceae (Brodribb et al. 2012). Why are tracheids so advantageous in cold climates?

Freeze–thaw-induced cavitation is a process by which air-bubbles frozen in the xylem sap expand during the thaw, and thus create an embolism in functional xylem conduits. The process begins when during freezing, air is pushed out of the ice crystal lattice, coalesced into bubbles and thus trapped in the frozen xylem sap (Sevanto et al. 2012). During the thaw, as transpiration reintroduces tension into the water column and the xylem regains functionality, the bubbles may either expand and fill the conduit with a mixture of air and water vapor, or they may collapse, with air redissolving back into the xylem sap. Which of the two options occurs is in large part determined by the xylem tension during the thaw (P_x) and the dimensions of the xylem conduits. Over two decades worth of research has shown that xylem conduit dimensions are mechanistically related to species' vulnerability to freeze–thaw cavitation (Ewers 1985; Davis et al. 1999; Pittermann and Sperry 2003).

The classic bubble-expansion mechanism rests on the relationship between P_x and the bubble pressure P^*, which is the combined pressure of the surface tension (t) and the air/water mixture (P_b, assumed to be a relative 0 MPa) of a bubble in liquid sap (Domec 2011). P^* is directly related to the diameter of an air-bubble (D_b) whereby

$$P^* = -4t / D_b + P_b \tag{2.1}$$

For a bubble to expand and nucleate cavitation, P_x must be more negative than P^*, the bubble's equilibrium pressure. Equation 2.1 reminds us that the larger the bubble, the lower the P^* and the greater the likelihood of bubble expansion under mild P_x. Accordingly, conifers with small tracheids were reported to be hardly susceptible to freeze–thaw-induced embolism (Hammel 1967; Sucoff 1969; Sperry and Sullivan 1992; Sperry et al. 1994; Davis et al. 1999; Feild and Brodribb 2001; Feild et al. 2002).

Several studies have shown that species with large-diameter conduits are more vulnerable to freeze–thaw-induced cavitation than those with narrower vessels or tracheids. Presumably, this is because the size of the bubble is directly proportional to the distance that the ice front must travel, so wider conduits lead to larger bubbles. This process is largely independent of conduit length. Angiosperms and conifers with equal-diameter vessels and tracheids show similar losses in conductivity at a given P_x during the thaw. Indeed, conduits wider than 43–44 μm will embolize during a mild P_x of −0.5 MPa (Davis et al. 1999; Pittermann and Sperry 2003). However, this critical diameter is predictably reduced to values below 18 μm under more negative thaw xylem pressures, which have been observed to vary between −1 and −4 MPa in nature (Pittermann and Sperry 2006 and literature cited therein). Aside from *Taxodium distichum* and *Pinus caribaea*, few conifers have branch tracheids that exceed 20 μm in diameter so they are well adapted to high-elevation habitats and the north-temperate and boreal regions where freeze–thaw cycles are a seasonal, or even daily occurrence during the winter season (Feild and Brodribb 2001; Schoonmaker et al. 2010). Tracheids in roots may be above 40 μm in diameter, but they are often insulated by soil and snow, and experience fewer freeze–thaw events than stems.

Repeated freeze–thaw events in conjunction with drought may cause higher loss of conductivity than single freeze–thaw events (Mayr et al. 2003a). Timberline conifers are exposed to more than 100 freeze–thaw cycles per winter; these frost cycles in combination with low water potentials cause up to 100 % loss of conductivity in *Picea abies* and other species (Mayr et al. 2006). Embolism formation upon freeze–thaw events amplified by drought stress was also reported in *Pinus* and *Larix* species (Sparks and Black 2000; Sparks et al. 2001). It is still unclear if increasing conductivity losses on repeated freeze–thaw cycles reflect stochasticity of the underlying bubble-expansion mechanism or if additional processes are involved. Ultrasonic emission analyses indicate that cavitation events are already initiated during freezing (Mayr et al. 2007; Mayr and Sperry 2010) and that minimal temperatures of a frost cycle are of relevance for bubble formation (Charrier et al. 2014).

Freeze–thaw events can cause very complex hydraulic patterns in conifers as observed at the alpine timberline: When the soil and/or trunk base are frozen, water supply is blocked, which can last for months in extreme environments (Fig. 2.1c). Evergreen conifers then have to keep stomata closed during winter and require a cuticular protection which sufficiently minimizes water loss as long as water supply is blocked (Michaelis 1934; Tranquillini 1976). However, overheating of needles, limited cuticular maturation, ice blast, or insufficient stomatal closure cause a slow but permanent and thus substantial decrease in water potential (Mayr et al. 2012). In parallel, freeze–thaw events lead to a segmentation of the trees' hydraulic system, as frozen xylem sections separate needles from branches and branches from the trunk. This segmentation changes in diurnal courses, so that timberline conifers show complex and dynamic patterns in water potential which, in turn, influence the formation of freeze–thaw-induced embolism (Fig. 2.11).

2.4 Phenotypic Plasticity

Much of the data discussed above refers to variation of traits across species. There is less information on intraspecific variability of hydraulic traits. Chapter 4 describes phenotypic plasticity with regards to hydraulic traits in *Populus* genotypes. How much plasticity exists in conifer species? In a study on 12 Scots pine (*Pinus sylvestris*) populations sampled along a climatic gradient in Western Europe, variability across sites was high for K_{smax} and leaf specific xylem conductivity (LSC), but not for P_{50}, midday water potential, mean tracheid diameter, and wood density (Martínez-Vilalta et al. 2009). The stability of midday water potentials (isohydric behavior) was a consequence of reducing the leaf-to-sapwood area ratio (A_L:A_S) with decreasing water availability, and possibly other factors. The study on Scots pine could not resolve how much of the observed variability in hydraulic traits was

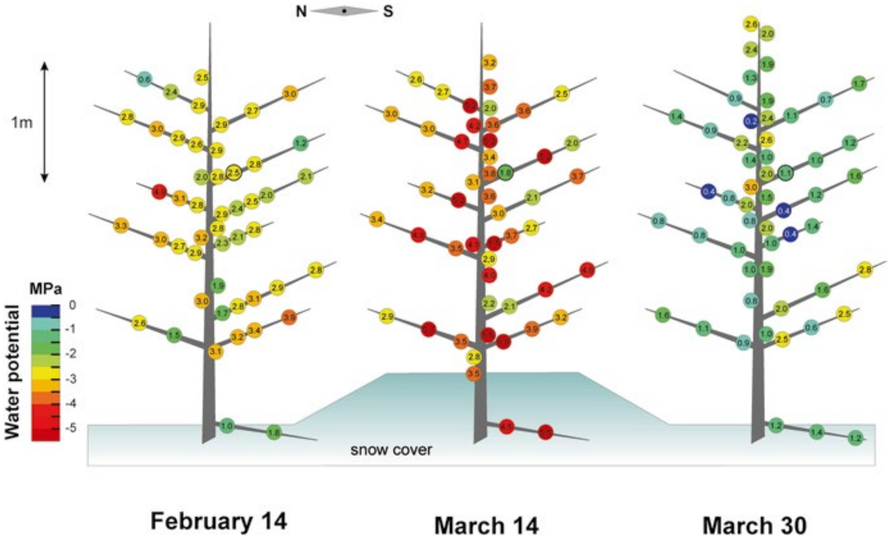

Fig. 2.11 Pattern in water potential during winter 2006 at the alpine timberline (2,035 m). Samples (*end twigs*) were taken from north and south exposed branches of one *Picea abies* tree in February as well as mid- and end of May and measured with the Scholander technique. Modified after Mayr and Charra-Vaskou (2007)

genetic in origin or the result of phenotypic plasticity (Martínez-Vilalta et al. 2009). Common garden experiments are useful in shedding light on this question.

Recent common garden experiments with interior spruce (*Picea glauca* and *Picea engelmannii*) and lodgepole pine (*Pinus contorta*) seed sources studied variation in frost hardiness and seedling growth. Most of the trait variation existed within populations. There was a remarkable degree of genetic diversity in the measured traits, implying a high evolutionary capacity to adapt to new environmental conditions (Liepe 2014). This is an interesting finding, and it raises the question how much genetic diversity exists for key hydraulic and wood anatomical traits, such as P_{50} and mean tracheid diameter.

A study on eight populations of *Pinus canariensis* growing at two common garden sites found considerable variability in P_{50} and other traits, and this was largely the result of phenotypic plasticity (López et al. 2013). Variability in hydraulic traits was also examined in six *Pinus pinaster* populations growing at a mesic and a xeric site (Corcuera et al. 2011). P_{50} and K_{smax} were significantly lower in the xeric site, and these shifts were mainly attributed to phenotypic plasticity. By contrast, wood density was genetically controlled and was not affected by the growing conditions.

Substantial phenotypic plasticity in vulnerability to cavitation and other important hydraulic traits was also found in other studies. For instance, loblolly pine (*Pinus taeda*) trees growing on loam versus sand soil exhibited phenotypic plasticity in P_{50}, root-to-leaf area ratios (A_R:A_L), and other traits (Hacke et al. 2000). Another study on loblolly pine found that nutrient addition caused an over 50 % reduction in A_R:A_L relative to control trees (Ewers et al. 2000). Reduction in A_R:A_L

was primarily due to a large increase in leaf area with improved nutrition. Changes in A_R:A_L are important, because they impact the potential for water uptake during soil drought. Schoonmaker et al. (2010) studied hydraulic acclimation to shading in four boreal conifer species. Open-grown and understory trees differed in many wood anatomical and hydraulic traits. One of the most profound changes occurred at the pit level. Shaded trees had, on average, larger pores in the margo than open-grown trees (Fig. 2.5). More porous pit membranes compensated for narrower tracheids in shaded trees, but also contributed to increased vulnerability to cavitation.

These studies suggest that conifers exhibit considerable potential for acclimating to different environments. Changes may occur at various levels, from shifts in A_R:A_L and A_L:A_S ratios to microscopic changes at the pit level. However, the piñon mortality described in Sect. 3 indicates that there are genetically determined limits to drought tolerance. While water loss can be regulated by the amount of leaf area and/or via stomatal closure, the potential of xylem to become more resistant to drought-induced cavitation during development appears to be rather limited. Limits to phenotypic plasticity may also constrain the height growth of giant conifers (Koch et al. 2004). To the extent that the water potential at the top of tall trees differs from the potential at the base of the tree, plasticity in wood structure and function will be required to adequately supply leaves with water.

2.5 Needle Structure and Water Movement in Needles

Needle architecture in conifers has been described as canalized and being limited in venation patterns compared with angiosperm leaves (Brodribb et al. 2012). While the diversity of venation patterns is limited, conifer needles are marvels in terms of tissue complexity and longevity. Huber (1947) pointed out that we can find many different cell types in a small cross section of a pine needle and viewed pine needles as some of the most complex structures in all of plant anatomy. Many structure–function relationships related to water and assimilate transport remain to be explored. In *Pinus longaeva*, needles remain alive on branches for 30 or more years. With advancing needle age, little or no change in the number of xylem cell layers was observed, but there was a significant increase in the layer of phloem cells (Ewers 1982). Hence, needles produced secondary phloem but no secondary xylem. In *Pinus longaeva*, newly produced phloem cells seem to continually replace dying phloem cells. The work of Ewers (1982) also implies that needle xylem can remain functional for many years.

Needles have been reported to be more vulnerable to dehydration-induced declines in hydraulic conductance than stems (Johnson et al. 2009; Johnson et al. 2011; McCulloh et al. 2014). Changes of needle hydraulic conductance may be caused by cycles of embolism and refilling (Woodruff et al. 2007; Johnson et al. 2012), reversible collapse of tracheids (Cochard et al. 2004; Brodribb and Holbrook 2005; Zhang et al. 2014), changes in the membrane permeability of bundle sheath cells (Laur and Hacke 2014), and other changes in the properties of living cells (see Chap. 10).

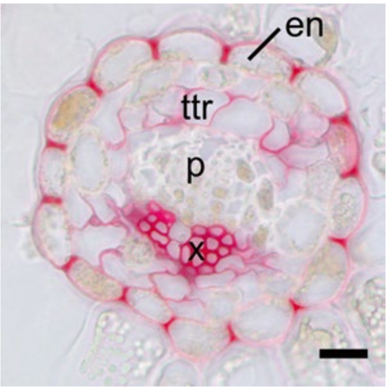

Fig. 2.12 Light microscopy image of a *Picea glauca* needle cross section. The section was stained with phloroglucinol-HCl; lignified cells walls are shown in *red*. Lignin was detected in radial cell walls of the endodermis (*en*), transfusion tracheids (*ttr*), and in xylem tracheids (*x*). *Bar* = 20 µm. From Laur and Hacke (2014)

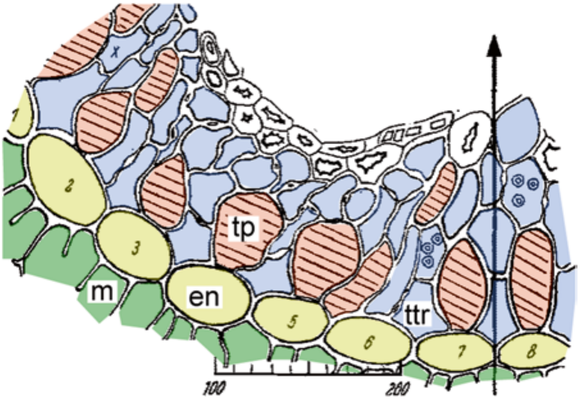

Fig. 2.13 Cross section of a pine needle (*Pinus nigra*). Modified after Huber (1947). Endodermis cells (*yellow*) are numbered (#*1*–*8*). Transfusion tracheids (*blue*, *ttr*) typically face the radial walls of the endodermis cells. Transfusion parenchyma cells (*tp*, *orange*, marked with *hatched lines*) are in contact with the median endodermis cell walls. *m* mesophyll (*green*). The *arrow* points to the center of the needle

As shown in Fig. 2.12, axial needle xylem of *Picea glauca* is surrounded by phloem and transfusion tissue. The work of Zhang et al. (2014) suggests that transfusion tissue may play an important role in needle hydraulics. This tissue includes transfusion tracheids, which serve in water storage and radial transport between the axial xylem and the bundle sheath (Fig. 2.13). Transfusion tracheids of *Taxus baccata* needles undergo reversible collapse in response to dehydration–rehydration cycles, and these volume changes were linked to reversible changes in leaf hydraulic conductance (Zhang et al. 2014). The reversible shrinkage of these cells may impact

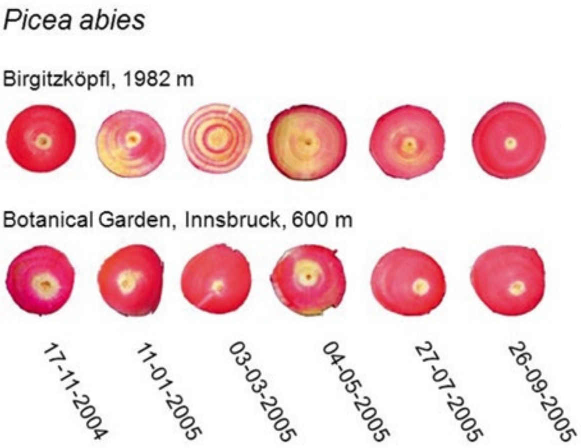

Fig. 2.14 Dye staining of branch cross sections of *Picea abies*. Branches were harvested from trees at low and high elevation in winter 2004/2005 and stained with Phloxine-B. *Red* areas indicate functional xylem, *non-stained* areas are embolized (Schmid and Mayr, unpublished)

the xylem pressure of axial tracheids. More work will be necessary to validate the existing hydraulic and imaging techniques that are suitable for studying needles, and to develop novel empirical methods and modeling approaches for studying needle hydraulics. Water potential measurements on a fine spatial and temporal scale would be helpful in interpreting some of the reported changes in needle hydraulic conductance and in determining the optimal needle transport capacity that minimizes the pressure drop per given investment in xylem (Zwieniecki et al. 2006).

Aquaporins (AQPs) are present in various needle tissues (see Laur and Hacke 2014 for details), including the bundle sheath. These water channels likely play a key role in facilitating radial water exchange between vascular and photosynthesizing needle tissue. Individual AQP genes of *Picea glauca* had different tissue distribution patterns of expression; yet all four of the studied genes showed expression in phloem cells (Laur and Hacke 2014). The prominent occurrence of AQPs in needle phloem suggests a role for water channels in phloem loading/unloading.

Needles are capable of taking up water from fog, intercepted rainfall, or melting snow (e.g., Burgess and Dawson 2004; Breshears et al. 2008a). Needle water uptake appears to play an important role in timberline conifers, which recover hydraulic conductivity in late winter and early spring, even when soils remain frozen. The needles of timberline trees are able to take up water from melting snow, and this water contributes to embolism repair in branches (Mayr et al. 2014). At the time of refilling, AQPs appear in the needle phloem and endodermis indicating a role in water uptake and the refilling process. Figure 2.14 shows a series of dye-perfused stem cross sections of *Picea abies* with functional xylem throughout the year at low elevation but remarkable winter embolism at the timberline. The entire cross section is refilled so that full functionality is restored for the vegetation period. The dye perfusion experiments shown in Fig. 2.14 indicate that conifer stems can recover hydraulic conductivity in late winter and early spring, even when soils remain frozen.

3 Conifer Hydraulic Architecture: How the Xylem Works in the Context of the Whole Tree

The performance of xylem in a live plant depends not only on the properties of the material, but on the distribution of water potentials within the plant at any time and how that affects physiological processes like photosynthesis and growth. The distribution of water potentials, in turn, depends on both the soil water availability and the atmospheric vapor pressure deficit, but also on the plant directly: the amount of xylem (sapwood width, length of the path), the variation in xylem properties within the plant, the size of the root system, the leaf area, capacitance (how much water will come out of storage per MPa water potential), and physiological behavior like the triggers of stomatal opening and closure. Moreover, the environmental factors and some of the plant-related factors will change in a cyclical manner (with seasons and phenology, for example), and others will change on a finer time scale. We have a relatively good understanding of how the plant-related factors should affect hydraulic performance in general. There is still much to learn, however, about the regulation and coordination of processes that contribute to the observed water potentials throughout a plant.

3.1 Leaf Specific Xylem Conductivity

Leaf specific xylem conductivity is a property that incorporates some of the architectural information about the plant into hydraulic information. The LSC is the hydraulic conductivity of a stem segment normalized by the leaf area distal to the segment, rather than by the stem cross-sectional area (Tyree and Ewers 1991). Whereas K_{smax} tells how "efficient" the material is at allowing water to pass, LSC tells how much water transport can occur per leaf area. The higher the LSC, the lower the water potential gradient required to maintain a particular transpiration rate.

In conifers, LSC generally increases greatly with stem diameter (Tyree and Ewers 1991), meaning that branches tend to have lower, LSC than the trunk (Domec et al. 2012). In branches of *Juniperus communis* trees, LSC and K_{smax} were low at the base, increased toward the distal parts and decreased again near the branch tips (Beikircher and Mayr 2008). These patterns are controlled in part by differences in tracheid dimension. One of the consequences of such patterns of LSC is the development of steep water potential gradients in smaller diameter branches (Tyree and Ewers 1991 and literature cited therein). Small distal branches are also the parts of the tree that are the least buffered from environmental conditions (sun, wind, drought), and thus are worthy of more study to better understand how entire plants deal with drought stress, and to better understand the process of branch die-back and death during drought.

A physical map of the water potentials at the apices of all the branches in a tree may have a strong relationship with a physical map showing the amount of extension growth of the stems, with more growth occurring where water is more available.

During the growing season, these ultimate water potentials depend on the flow path's resistance and on the leaf area supplied. We do not have a strong understanding of the feedback between growth and wood development—does a low water potential direct the formation of a bud that will make a small leaf area? Most research on conifers has been conducted in trees with a pyramidal form that results from a dominant central leader and spreading angled branches off the leader. It would be interesting to better understand the relationship of tree form, branch growth, and hydraulic architecture by having more research in coniferous species that do not have this pyramidal form.

3.2 The Transport Network

Within a woody plant, water moves from the root to the stomatal cavity through a network of xylem conduits. Much research attention has focused on the optimal form of that network for transporting water with the least biomass investment. It has long been known that the bole has higher K_{smax} than branches, and that the higher the order of branch, typically the lower the K_{smax} (e.g., Dunham et al. 2007; Domec et al. 2012). This pattern results largely from the positive correlation of tracheid diameter and stem diameter (Petit et al. 2009). McCulloh et al. (2010) concluded that conifers had a pattern of change in stem conductivity with stem size that was intermediate between the steep change in ring-porous hardwoods, and the shallower change in diffuse-porous hardwoods.

Another issue related to the transport network is the pathways by which water moves radially. Assuming that water is delivered primarily to the outer growth ring in roots and that it exits from xylem attached primarily to the outer three or four growth rings in the shoot (Maton and Gartner 2005), but that it ascends the tree through many growth rings, one can ask how that water moves in the radial direction, near both at the source and transpiration ends. In a typical conifer, the bordered pits are mostly on the tracheids' radial walls, which means water can move most easily in the tangential direction (e.g., laterally, within a ring). In some species there is a small amount of tangential wall pitting in the last-formed latewood and the first-formed earlywood (Panshin and Zeeuw 1980; Kitin et al. 2009), presumably facilitating movement between rings. Barnard et al. (2013) used dye to visualize the radial water movement, and found no evidence that water movement occurred through ray tracheids.

3.3 Transport Safety and Drought-Induced Cavitation

Cavitation resistance potentially confers drought tolerance because maintenance of water-filled conduits during drought ensures sufficient supply of water to leaves. The greater the cavitation resistance, the higher the potential for gas exchange and for extracting water from a drying soil (Sperry et al. 1998). Across Cupressaceae species, the P_{50} of stems was correlated with the minimum growing-season precipitation of the species' native range (Pittermann et al. 2012). Similar relationships have also been found for southern hemisphere conifers (Brodribb and Hill 1999).

A number of case studies on the piñon-juniper communities of the south-western USA revealed how cavitation resistance of conifers relates to habitat and gas exchange. Utah juniper (*Juniperus osteosperma*) dominates in the lower, drier sites while Colorado piñon (*Pinus edulis*) is more common as precipitation increases with elevation. Juniper is generally considered as the more drought-tolerant species, which agrees with juniper having more resistant xylem than piñon (Linton et al. 1998). Tracheid diameters in juniper were narrower than in piñon, and the hydraulically weighted tracheid diameter was correlated with cavitation resistance.

The two species showed contrasting dynamics in terms of xylem pressure and gas exchange. *P. edulis* exhibited pronounced stomatal closure during drought, which allowed plants to maintain high xylem pressures. Due to its relatively vulnerable xylem, piñon appeared to be operating near its hydraulic limits (Linton et al. 1998). These differences in water relations between the two species may explain why piñon disappears from piñon-juniper woodlands at lower, drier elevations.

The Linton et al. (1998) study revealed that co-occurring plants may not only differ in their resistance to cavitation, but also in their strategies for avoiding cavitation. The latter may be just as important as cavitation resistance per se for predicting how species may cope with climate change and associated changes in moisture availability and how co-occurring species influence each other under drought-stress conditions. An isohydric strategy might fail when neighboring plants risk high water losses and a reduction of soil water potentials.

A 4-year drought (from 2000 to 2003), which was associated with anomalously high temperatures, triggered extensive mortality of *P. edulis* (Breshears et al. 2005). The die-off likely relates to the greater xylem vulnerability of piñon relative to juniper, and the water use strategies that are associated with these differences in cavitation resistance. While *P. edulis* exhibited higher sap flux than *J. osteosperma* under favorable conditions, *P. edulis* used isohydric stomatal control to avoid cavitation during periods of water shortage. *J. osteosperma*, by contrast, sacrificed high sap flux rates for greater resistance to cavitation and exhibited anisohydric stomatal regulation (West et al. 2008). The high resistance to drought-induced cavitation in *Juniperus* species helps explain the survival of junipers during recent extreme droughts and why they have been able to expand into drier environments across the western and central USA over the last century (Willson et al. 2008).

Prolonged stomatal closure in *P. edulis* in response to persistent water stress may lead to a depletion of carbon reserves (Plaut et al. 2012; Sevanto et al. 2014). This may make trees susceptible to beetle attack, and may eventually lead to mortality (Breshears et al. 2008b; West et al. 2008). Drought-stressed trees may also lack the carbon reserves that are required to reestablish hydraulic function after a drought (Brodribb and Cochard 2009), i.e., trees may not be able to refill embolized xylem and grow new fine roots (Plaut et al. 2012). In addition, it remains to be tested if vulnerability to cavitation increases in conifer xylem that previously cavitated and refilled (so-called "cavitation fatigue," Hacke et al. 2001a).

The studies on the piñon-juniper woodlands indicate that it is useful to interpret cavitation resistance in the context of stomatal behavior. As shown for piñon, trees may not necessarily die from outright hydraulic failure (McDowell et al. 2013; Sevanto et al. 2014), but rather from the consequences that arise from the need to avoid hydraulic failure. Accumulation of hydraulic deterioration as observed in trembling aspen (Anderegg et al. 2013) may also be important in conifers. Knowing the vulnerability curves (or the P_{50}) of different species and plant organs is a prerequisite for understanding and predicting mortality patterns. Recent research comparing traits of *Pseudotsuga menziesii* trees after a severe drought in France showed slightly higher wood densities in the survivors (Ruiz Diaz Britez et al. 2014). These results are consistent with research showing that clones of the same species that had higher density also had more negative values of P_{50} (Dalla-Salda et al. 2009).

What structural features are associated with greater cavitation resistance and why does the P_{50} of conifer stems scale with the minimum xylem pressure measured in plants under natural conditions (Choat et al. 2012)? While more cavitation-resistant xylem will be required in dry habitats, it may not be advantageous in mesic habitats. There are at least two costs associated with resistant xylem. First, species that are resistant to drought-induced cavitation tend to have narrower tracheids and lower K_{smax} than species with vulnerable xylem (Fig. 2.15a). We caution, however, that the diameter-vulnerability trends are not always observed in other data sets. Second, greater cavitation resistance was associated with greater wood density, an excellent correlate of wood strength (Fig. 2.15b) (again, not always observed in other data sets), which is based on respective carbon investments.

A priori, one may not expect to find either of these relationships. Wood density reflects earlywood and latewood densities weighted by their respective proportion within a ring, whereas the hydraulic properties of a sample are mainly determined by the earlywood (Domec et al. 2009). Further, it is generally assumed that cavitation resistance is primarily determined by properties of inter-tracheid pits, and it is not clear how pit properties would scale with wood density and tracheid diameter. Why then have correlations between P_{50}, wood density, and tracheid diameter emerged in many datasets (Hacke et al. 2004; Pittermann et al. 2006b, 2012; Domec et al. 2009; Rosner 2013)?

A link between P_{50}, conduit reinforcement, and wood density can be explained in the light of cohesion-driven water transport. The more resistant the xylem is to cavitation, the more negative the xylem pressure the plant can sustain, and the stronger the tracheid walls must be. Bending stresses arise in the double wall between water- and air-filled tracheids (Hacke et al. 2001b). The thicker the double wall (t) relative to its span (b), the greater the reinforcement against collapse. One may therefore expect conduit reinforcement (t/b) to scale with the pressure range tracheids must cope with. This pressure range is limited by cavitation. A riparian *Taxodium* tree has vulnerable xylem, wide tracheids, and will require less conduit reinforcement than *Widdringtonia cedarbergensis*, which has extremely resistant xylem ($P_{50} = -11.3$ MPa, Pittermann et al. 2010). Comparing xylem cross sections of these taxa demonstrates that this expectation is justified (Fig. 2.2).

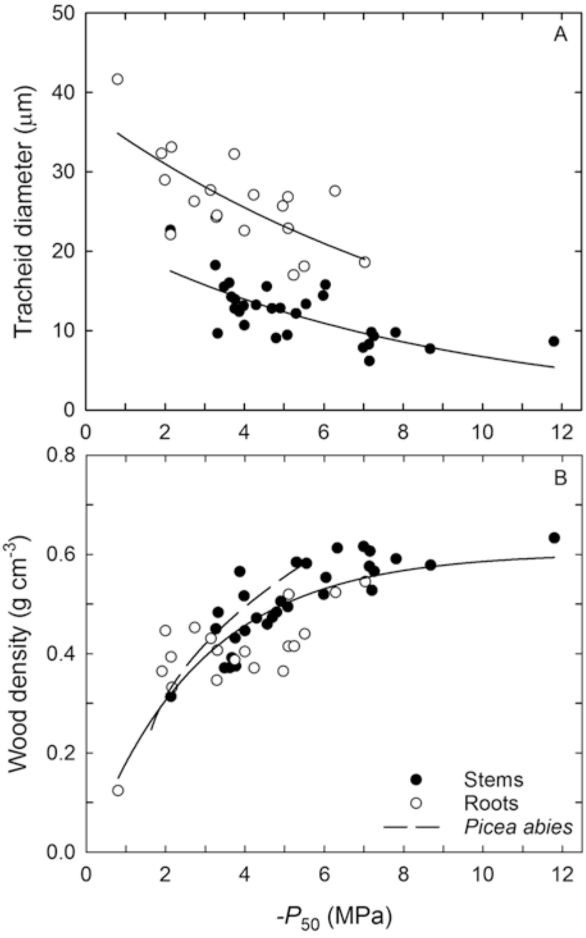

Fig. 2.15 Mean tracheid diameters (**a**) and wood densities (**b**) of roots (*open symbols*) and stems (*closed symbols*) of northern hemisphere conifer species as a function of their cavitation resistance (expressed as the xylem pressure inducing 50 % loss of hydraulic conductivity, P_{50}). The data was taken from various publications (Hacke et al. 2001b); Pittermann et al. 2006b; Hacke and Jansen 2009; Schoonmaker et al. 2010). The *dashed curve* in (**b**) is a regression of data presented by Rosner et al. (2014, their Fig. 2a), and is based on samples taken at various heights from 5- to 50-year-old Norway spruce (*Picea abies*) trees growing in Sweden, Norway, and Germany. See Rosner et al. (2014) for details

In Pinaceae and Cupressaceae species, the significant increase in conduit reinforcement and wood density with more negative P_{50} translated into decreasing tracheid diameters with more negative P_{50}. This is because the variation in t/b in the data set of Pittermann et al. (2006b) was mainly driven by variation in tracheid diameter rather than wall thickness (but see Bouche et al. 2014). Trends in tracheid diameter impact transport efficiency, which explains why attaining greater mechanical reinforcement comes at the expense of reduced K_{smax} (Pittermann et al. 2006b, 2012). These structure–function trade-offs likely explain the correlations shown in Fig. 2.15.

However, Pittermann et al. (2006b, 2012) found that southern hemisphere species were quite different from the northern hemisphere conifer species featured in Fig. 2.15. The wood of Podocarpaceae, Araucariaceae, and southern hemisphere Cupressaceae appears to be overbuilt for bearing transport stress, making their xylem expensive and hydraulically inefficient. Functionally, this means that for an equivalent P_{50}, conduit diameters and t/b ratios are much higher in these taxa than in north temperate conifer endemics, reminding us that xylem attributes are somewhat decoupled from transport efficiency in these trees (Pittermann et al. 2006a, b). This suggests that selection for efficient water transport is not as strong in these taxa. Given that the sampled trees occupied humid, mesic habitats in which water limitation is unlikely, it is possible that selection acted on xylem attributes that are more related to rot resistance and longevity. In contrast, tracheid walls in the needles of *Pinus* and *Podocarpus* species were found to be insufficiently reinforced and thus to show cell wall deformation before cavitation (Cochard et al. 2004; Brodribb and Holbrook 2005).

The wood density versus P_{50} relationship has far-reaching consequences due to the significance of wood density for various aspects of tree physiology (for a discussion of some of these, see Pittermann et al. 2006b; Lachenbruch and McCulloh 2014). To the extent that wood density is related to growth and drought sensitivity, the data shown in Fig. 2.15b has potential implications for tree breeding. Rosner et al. (2014) discussed if wood density can be used as a screening trait for drought sensitivity in Norway spruce. They concluded that density is a highly predictive trait for cavitation resistance of trunkwood in Norway spruce (see the dashed curve in Fig. 2.15b). However, they cautioned that the relationship between density and P_{50} is only valid when mechanical demands do not interact with hydraulic demands. Rosner et al. (2014) pointed out that rapid growth is often a principal criterion for tree breeding. Selecting for growth may lead to lower transport safety, at least in species like Norway spruce, in which growth rate is inversely related to wood density. In the light of global climate change it may be safer to select for higher densities, even at the cost of slower short-term growth under favorable conditions.

3.4 Variations of Xylem Safety Across Plant Organs and with Height

How does cavitation resistance vary across plant organs? Several hypotheses predict how xylem structure should change along the root-to-branch water transport pathway to optimize tree hydraulic efficiency and protection from embolism (Comstock and Sperry 2000; McCulloh and Sperry 2005), but there are only a few studies that have sampled more than two points along the entire pathway (Domec and Gartner 2002b; McElrone et al. 2004; Burgess et al. 2006; Dunham et al. 2007). Small diameter roots are typically more vulnerable than small diameter stems and branches (Fig. 2.9, Sperry and Ikeda 1997; Hacke et al. 2000; McElrone et al. 2004; Domec et al. 2009), consistent with roots experiencing less negative xylem pressure than above-ground plant organs. In some juniper species, growing in very dry habitats, however, vulnerability does not differ between roots and stems (Linton et al. 1998; Willson et al. 2008).

There are considerable differences in hydraulic properties between small and large roots. Smaller roots of loblolly pine were more vulnerable than larger roots (Fig. 2.9). This trend is consistent with findings of Dunham et al. (2007), who

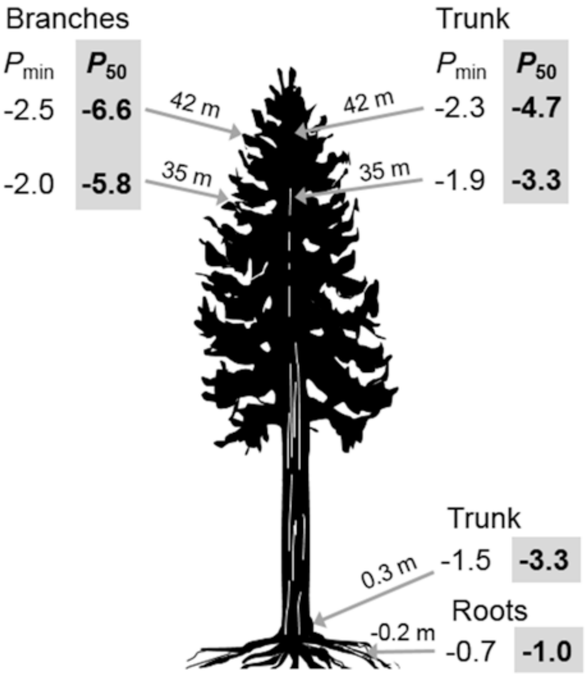

Fig. 2.16 Illustration of the variation in minimum in situ xylem pressure (P_{min}) and xylem pressure causing 50 % loss of hydraulic conductivity (P_{50}) in a large Douglas-fir tree. Both P_{min} and P_{50} become more negative with increasing height and increasing lateral distance from the trunk. Based on Domec et al. (2009) and Dunham et al. (2007)

reported that small/young Douglas-fir roots embolized much more readily than the large structural roots close to the trunk. Roots may be very variable in terms of xylem anatomy and hydraulic properties. This variability is also observed along the trunk (Schulte 2012b) and between branches of different heights. For instance, the mean tracheid diameter in branches of a 90 m *Sequoiadendron giganteum* was correlated with xylem pressure measured at dawn; branches from higher parts of the crown exhibited more negative xylem pressure as well as narrower tracheids (Rundel and Stecker 1977). The authors concluded that the advantages of narrow tracheids under water stress conditions relate to properties of thin-walled tubes in resisting strong mechanical tensions. Studies on giant *Sequoia sempervirens* and *Pseudotsuga menziesii* trees found that air-seeding pressures became substantially more negative with increasing height, a trend observed in branches (Koch et al. 2004; Burgess et al. 2006; Domec et al. 2008) and trunk xylem (Domec et al. 2008). This trend is expected based on the progressive drop in xylem pressure with height (Koch et al. 2004). Much remains to be learned about this variation and how it relates to the water use strategy of a plant.

In large Douglas-fir trees, trunk xylem was more vulnerable and had wider and longer tracheids than branch xylem sampled at the same height (Domec and Gartner 2002a; Dunham et al. 2007) (Fig. 2.16). Large roots (cambial age ~42 years) were very similar to samples taken from the trunk (cambial age ~52 years) in terms of xylem anatomy and hydraulic properties, including P_{50} (Dunham et al. 2007). Conifer branches generally appear to be hydraulically safer than the trunk and small roots.

In *Picea abies*, the leader shoot was found to be more resistant to drought-induced embolism than nearby side branches (Mayr et al. 2003b). This trend is consistent with the need for more embolism-resistant xylem as the pressure drops along the flow path from the roots to the leaves. In each of these studies the decrease in P_{50} in the stems came at the cost of higher flow resistance than in the roots. The safety factor for xylem failure by air-seeding may be defined as the ratio of P_{50} to the minimum summer xylem pressure for a particular plant part (P_{50}/P_{min}). In Douglas-fir and Ponderosa pine, the safety factor was minimal in roots and intermediate in the trunk. Branches had the highest P_{50}/P_{min} ratio (Domec and Gartner 2002a; Domec et al. 2009). This agrees with a study on four conifer species growing in the Pacific Northwest region of North America (McCulloh et al. 2014). The study also reported that the vast majority of hydraulic conductance was lost by midday in needle-bearing shoots while essentially no embolism was predicted to occur in small diameter branches and trunks.

Closer inspection of Fig. 2.16 also reveals that the bases of the trees had lower safety factors for hydraulic failure than top parts. However, roots and trunk bases may exhibit relatively small fluctuations in xylem pressure because of buffering mechanisms related to redistribution of water in the soil and plant tissues (Domec et al. 2009; McCulloh et al. 2014). Small, vulnerable roots may regrow or may be refilled depending on soil moisture availability (Domec et al. 2004).

3.5 Conclusions

As we increase our understanding of conifer xylem, we come to appreciate both its simplicity and its elegance. The tissue contains only two basic cell types: tracheids (mainly axial, some radial) and parenchyma (mainly radial, some axial). It has only three main features that affect water transport: its aspect ratio, its cell wall thickness relative to lumen diameter, and its bordered pit frequency, geometry, and biomechanics. With small alterations in these three factors the material can orchestrate extremely different performance in terms of water transport, embolisms resistance, and capacitance. These small alterations are part of the adaptive traits that allow different species to occupy such disparate habitats as the edge of the permafrost, the high desert of the interior western USA, equatorial South America, and maritime zones in southern Europe. Likewise, these small alterations are also found, in some cases, in different ecotypes of the same species. Furthermore, within a species the same traits can be altered to confer adaptive changes as the functional role alternates between properties conferred by earlywood, and then latewood; in comparison of organs like branch tips, roots, and boles; and as a the plant grows from small to large.

The pits themselves are highly specialized valves that, through their varied within-plant frequency and geometry appear to control not only the spread of embolism (which would disable the water transport system), but the prioritization of delivery of water throughout a tree. Small changes in pit characteristics affect earlywood and latewood function, tangential transport within a single ring, radial transport of water from one growth ring to the next, the speed with which water is used by a tree, and which parts of a tree are hydraulically favored in times of low water availability. Pit characteristics vary by habitat and plant part. Thus, even though conifer wood, at first glance, is a rather uniform material, at the microscopic and functional levels, it is quite varied and gives rise to important differences in capabilities of the woody parts of a plant, which can have a major effect on plant performance.

Lastly at the level of the whole plant, there are several traits beyond wood structure that affect conifer hydraulic performance: the plant-controlled factors that contribute to transpiration (leaf area, stomatal control, cuticular water loss, capacitance), conductance (sapwood area, K_{smax}, pathlength for water transport), and water acquisition (root surface area, absorptive capacity). These traits can differ greatly among species, or by habitat for the same species. As shown above, the understanding of a plant's hydraulic architecture cannot be complete without these considerations, as well as some knowledge of non-plant controlled factors (e.g., pattern of water availability and vapor pressure deficit, and soil water-release characteristics).

There remain many intriguing gaps in our knowledge about how conifer hydraulic function works. There are questions of co-ordination during development (e.g., how are leaf-to-sapwood area ratios controlled) and co-ordination of physiological processes (how does stomatal control of transpiration at various water potentials relate to embolism formation in the roots, stems, and in foliage). There are signaling questions and questions of the extent to which traits can compensate for one another to deliver similar performances. These questions must affect our initial attempts to glibly state what a trait is "for" (e.g., what is the adaptive significance of a certain morphology) or our broad-brush attempts to answer questions of biogeography (e.g., why are there very few pines in the Coast Range of Oregon). Many fundamental advances will be forthcoming still. Currently, advances are resulting not only from experimental ecophysiological projects, but also from functional trait analyses of large datasets that make use of correlations that may not be directly causal. Advances may also result from the use of materials to be developed by molecular biology programs that make novel trait combinations or that knock out one set of capacities, thus calling into question what compensations will occur and how these compensations affect performance. The current and anticipated advances in understanding of conifer hydraulic architecture are likely to shed light on plant adaptation, habitat use, range of conditions an organisms or a species may occupy and the magnitude of changes that can be accommodated by individuals with various levels of traits. Such work will likely be of much value to land and natural resource managers, and will be of use for people working in a variety of areas such as tree breeding, development of urban landscape plant materials, bioremediation, greenhouse gases mitigation, and production of biomass of a variety of qualities for pulp, timber, and energy production.

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