

## SIZE AND FUNCTION IN CONIFER TRACHEIDS AND ANGIOSPERM VESSELS<sup>1</sup>

JOHN S. SPERRY,<sup>2,4</sup> UWE G. HACKE,<sup>2</sup> AND JARMILA PITTERMANN<sup>3</sup>

<sup>2</sup> Department of Biology, University of Utah, 257S 1400E, Salt Lake City, Utah 84112 USA; and

<sup>3</sup> Department of Integrative Biology, University of California, 4007 Valley Life Sciences, Berkeley, California 94720 USA

The wide size range of conifer tracheids and angiosperm vessels has important consequences for function. In both conduit types, bigger is better for conducting efficiency. The gain in efficiency with size is maximized by the control of conduit shape, which balances end-wall and lumen resistances. Although vessels are an order of magnitude longer than tracheids of the same diameter, they are not necessarily more efficient because they lack the low end-wall resistance of tracheids with torus-margo pits. Instead, vessels gain conducting efficiency over tracheids by achieving wider maximum diameters. End-walls contributed 56–64% to total xylem resistance in both conduit types, indicating that length limits conducting efficiency. Tracheid dimensions may be more limited by unicellularity and the need to supply strength to homoxylous wood than by the need to protect against cavitation. In contrast, the greater size of the multicellular vessel is facilitated by fibers that strengthen heteroxylous wood. Vessel dimensions may be most limited by the need to restrict intervessel pitting and cavitation by air-seeding. Stressful habitats that promote narrow vessels should favor coexistence of conifers and angiosperms. The evolution of vessels in angiosperm wood may have required early angiosperms to survive a phase of mechanic and hydraulic instability.

**Key words:** ecological wood anatomy; vascular structure and function; water transport; wood biomechanics; xylem cavitation.

Plant xylem transport, being in essence a physical process, can be fully understood only by invoking biomechanics. The problems of frictional resistance, cavitation, and conduit collapse are biomechanical in nature, as are the adaptive solutions to these problems. We know much more about comparative wood anatomy than we do about comparative wood function. Trade-offs in function are especially important because they presumably drive the evolution of anatomical diversity. The field of evolutionary and ecological wood anatomy is rife with hypotheses waiting to be tested. The structure–function knowledge gap can be closed only by a combination of biomechanical and physiological study.

In this paper we focus on a simple but important trait: the size of the water-conducting unit, or conduit. Length, diameter, and wall thickness of conduits can influence xylem flow resistance and protection against cavitation and wall collapse. Complex trade-offs appear to exist between these three functions. In our recent publications, we have analyzed these trade-offs within either conifer tracheids (Pittermann et al., 2006a, b) or angiosperm vessels (Wheeler et al., 2005; Hacke et al., 2006) in secondary xylem. Here we take the opportunity to compare the results for these two very different conduit morphologies and update a previous theoretical treatment of the topic (Hacke et al., 2005).

Conifer and angiosperm wood make for an informative comparison. Conifer wood exploits the efficiency of multi-tasking. The tracheid functions not only in transport, but also in mechanical support. Although the unicellular tracheid type

of conduit is ancestral, the intertracheid pitting in conifers is derived because it has a torus-margo pit membrane. Angiosperm wood exploits the efficiency of specialization. The wood in all but a few basal groups is heteroxylous with an axial system composed of vessels for transport, a dense matrix of fibers (and tracheids in some species) for support, and varying amounts of axial parenchyma for storage and possibly also to assist in embolism repair. The evolutionarily advanced vessel type of conduit is multicellular, and intervessel pit morphology is quite diverse. The pit membrane, however, generally lacks the conspicuous specialization of the torus-margo membrane and at least superficially has a relatively homogenous texture.

Despite their qualitatively different structures and evolutionary histories, both wood types appear to be very successful. Angiosperms, of course, are much more diverse in growth form and species. Conifers, however, can form extensive forests and woodlands in cold, dry, and nutrient-limited environments. The largest and longest-lived trees are conifers. Trade-offs in wood structure and function may contribute to this coexistence, with no one wood type being uniformly superior across the world's ecological diversity.

### CONDUIT SIZE RANGE

Figure 1 shows the range of conduit diameter and length in our data sets of coniferous and angiosperm woods. The size and function values we report are based on interspecific and interorgan variation. The data points are mean values of often considerable variation within growth rings (Gartner, 1995; Domec and Gartner, 2002b). The wood was sampled from branches (and roots of some conifers) of 8–12 mm diameter and is biased towards juvenile xylem with typically smaller conduits than in adult wood. Conifer species, all trees, ranged from north-temperate Pinaceae and Cupressaceae to southern hemisphere Podocarpaceae and Araucariaceae (Pittermann et

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<sup>4</sup> Author for correspondence (e-mail: j.sperry@utah.edu)

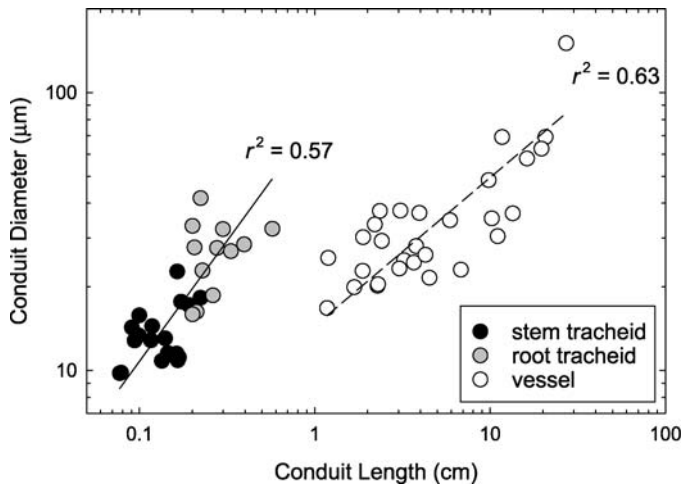


Fig. 1. Scaling of conduit diameter with length for conifer tracheids and angiosperm vessels. Data points are mean values for different species or organs; vessel data from stems only. Regression slopes (reduced major axis) were 0.87 in conifers and 0.53 in angiosperms and not different from the 0.67 scaling predicted to maintain the observed proportionality between lumen and end-wall resistivity ( $P > 0.05$  in conifers,  $P > 0.46$  in angiosperms). Data from Pittermann et al. (2005) and Hacke et al. (2006).

al., 2006a). Angiosperm species were eudicot shrubs, trees, and vines from numerous North American habitats and families (Hacke et al., 2006). Their vessels have simple perforation plates in most cases. Tracheid and vessel diameters represent the diameter of a conduit of average lumen conductivity as calculated by applying the Hagen–Poiseuille equation to measurements of conduit lumen diameter. Conduit length was measured in macerations (conifers, Mauseth and Fujii, 1994) or using a silicon-injection method (for vessels, Wheeler et al., 2005). Vessel length distributions are short-skewed (Zimmermann and Jeje, 1981), and means represent log-transformed data.

The largest difference between vessels and tracheids is in length rather than diameter (Fig. 1). Tracheids, being unicellular, were restricted to less than 6 mm in length, the maximum being in roots of *Pinus caribea* Morelet. Tracheids in adult stem wood reach a similar maximum length (Panshin and de Zeeuw, 1970) and so in terms of size, our juvenile root wood approximated the maximum tracheid sizes of adult trunk wood. Multicellular vessels, in contrast, were an order of magnitude longer, ranging from 1.17 cm in the montane evergreen shrub *Paxistima myrsinites* (Pursh) Raf. (Celastraceae) to 27 cm in the vine *Poureria montana* (Lour.) Merr. (kudzu, Fabaceae).

In contrast to length, diameter was more similar between tracheids and vessels. Tracheids ranged from 10 to 42  $\mu\text{m}$  in diameter in our data set, with larger averages up to 50–65  $\mu\text{m}$  reported for mature trunk wood (Panshin and de Zeeuw, 1970). Vessels had a minimum diameter of 17  $\mu\text{m}$  diameter in *Paxistima myrsinites* and overlapped considerably with the tracheid range. Vessels, of course, reach the larger maximum girth, and averaged 150  $\mu\text{m}$  in *Poureria montana*. Vessels with diameters in excess of 500  $\mu\text{m}$  occur in adult stems of tropical lianas (Zimmermann, 1983).

## CONDUIT SIZE AND CONDUCTING EFFICIENCY

Conduit diameter and length have major consequences for conducting efficiency. We define conducting efficiency as hydraulic conductance (a flow rate per pressure difference for water at 20°C) standardized for path length and cross-sectional area. Factoring out the influence of length on conductance yields a conductivity and further expressing it per cross-sectional area gives an “area conductivity.” The conduit-area conductivity represents conducting efficiency at the single conduit level (flow rate per conduit cross-sectional lumen area per pressure gradient).

The literature emphasizes the tremendous gain in conducting capacity from even a small increase in diameter (Zimmermann, 1983; Ewers, 1985; Tyree and Ewers, 1991). According to the Hagen–Poiseuille equation, the lumen conductivity increases with the fourth power of the lumen diameter. When the conductivity is expressed on a cross-sectional-area basis, the lumen area conductivity increases with the square of the conduit diameter. Measurements of lumen conductivity agree with Hagen–Poiseuille calculations, at least for vessels with simple perforation plates (Zwieniecki et al., 2001; Sperry et al., 2005). These considerations imply a significant gain in efficiency from modest increases in conduit girth.

What is not emphasized in the literature is that an increase in lumen conductivity does not necessarily increase the total conduit conductivity. Water not only flows through the lumen, but also through the narrow pits of the conduit end-walls. If an increase in conduit diameter is to cause a second-power increase in the conduit area conductivity, the end-wall conductivity must increase in concert (Schulte and Gibson, 1988; Lancashire and Ennos, 2002). Otherwise, an increase in diameter brings diminishing returns.

The length of the conduit is important because it influences the conductivity of the end-wall. The end-wall conductivity is the conductance through one end-wall standardized for the distance between the two end-walls of the conduit. The longer the conduit, the fewer end-wall crossings must be made per unit length, and so the greater is the end-wall conductivity. In theory, a conduit of a given diameter could become long enough to virtually eliminate the contribution of the end-walls to its conductivity. At this “saturating length” the conduit’s conductivity would equal its Hagen–Poiseuille lumen conductivity (Sperry and Hacke, 2004).

In practice, no conifer tracheid or angiosperm vessel in Fig. 1 approached this saturating length. In quantifying the contribution of lumen and end-wall to the total conduit conductivity, it is easier to use the reciprocal of conductivity, or the resistivity. Resistivities are additive when arranged in series, as is approximately the case for lumen and end-wall components of a conduit. In both conduit types, the end-walls contributed on average more than half of the total conduit flow resistivity (Fig. 2). End-walls accounted for  $64 \pm 4\%$  of the total resistivity in tracheids and  $56 \pm 2\%$  in vessels (mean  $\pm$  SE). Such a large end-wall limitation implies that conduit length is constrained in tracheids as well as in vessels.

The end-wall contribution in both conduit types was independent of conduit size because longer conduits were also wider (Fig. 1), and sufficiently enough to maintain the end-wall contribution nearly constant (Fig. 2). Theory predicts that diameter must increase with length to the 2/3 power to maintain a constant end-wall limitation if there is no size-dependent variation in the pit conductance per tracheid wall area

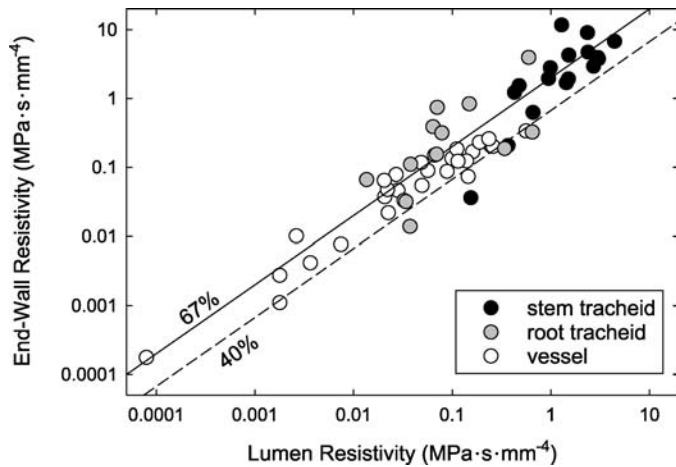


Fig. 2. Proportionality between end-wall resistivity and lumen resistivity in conifer tracheids and angiosperm vessels. Data points are mean values for different species or organs; vessel data from stems only. End-wall resistivity averaged  $64 \pm 4\%$  (mean  $\pm$  SE) of total resistivity across all tracheids, and  $56 \pm 2\%$  across all vessels. Diagonals show the 67% proportionality for optimizing conduit area conductivity under a length constraint (Fig. 4A) and the 40% optimal proportionality for a surface area constraint (Fig. 4B). Data from Pittermann et al. (2005) and Hacke et al. (2006).

(Lancashire and Ennos, 2002). This  $2/3$  scaling is consistent with the regression slope in both conduit types (Fig. 1), where the slope is from a reduced major axis regression because neither length nor diameter was controlled (Niklas, 1994). A size-independent end-wall contribution allows the conduit area conductivity to increase with the second power of the conduit diameter (Fig. 3A, reduced major axis regression), just as the Hagen–Poiseuille equation predicts for the lumen area conductivity (Fig. 3A, lumen conductivity line). However, because of the very substantial bottleneck of the end-wall pits, the conduit area conductivity is less than half the lumen conductivity across all sizes of vessels and tracheids (Fig. 3A, compare conduit and lumen conductivities).

While a constant end-wall contribution insures a second-power increase in conduit-area conductivity with diameter, why should the percentage of end-wall resistance seemingly converge on 56% for angiosperm vessels and 64% for conifer tracheids? In conifers, this percentage may reflect the optimization of conduit area conductivity under a conduit length constraint. This optimization is illustrated in Fig. 4A for a conduit where diameter is allowed to increase while length and end-wall conductivity per wall area is held constant. There is an optimal diameter that maximizes the conduit area conductivity (solid curve), at which point the end-wall contributes 67% of the total resistivity (dashed curve). Below this diameter, the area conductivity falls because it is lumen-limited. Above the optimal diameter, the area conductivity falls because it is end-wall limited: the conduit's cross-sectional area increases more than its conductivity. Regardless of the exact conduit length or pit conductivity, when these variables are held constant the conduit area conductivity is greatest at 67% end-wall resistivity (Pittermann et al., 2006a; Eqs. 8, 9).

The optimal 67% end-wall percentage is similar to the  $64 \pm 4\%$  average value measured for tracheids (Fig. 2, 67% diagonal; Fig. 4, solid circles), suggesting that tracheid diameters are optimized on average to maximize conducting

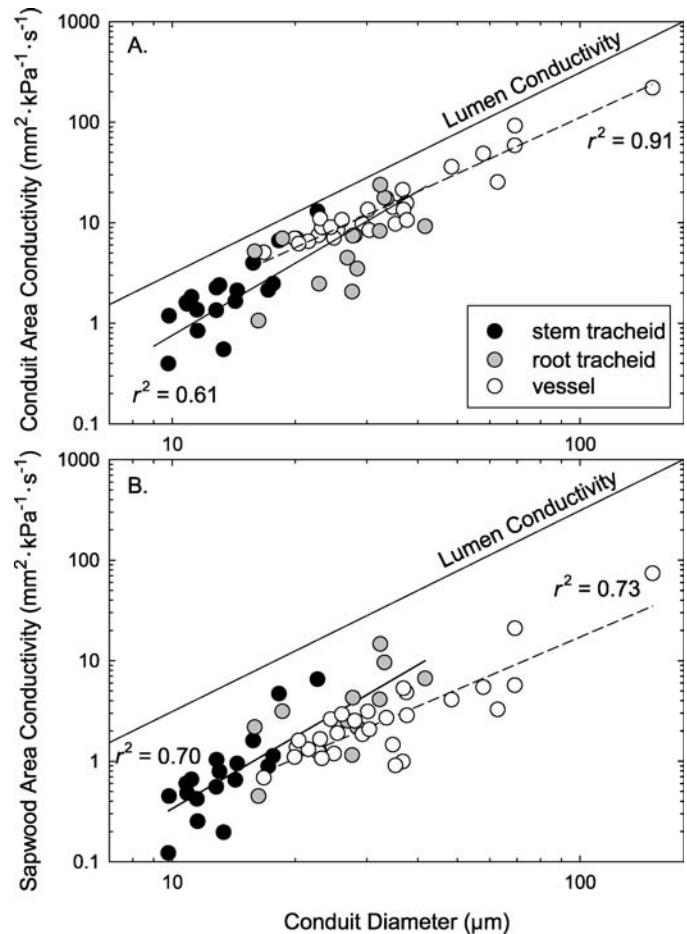


Fig. 3. Scaling relationships between hydraulic conductivity and conduit diameter. (A) Conduit area conductivity (conductivity per lumen area) and conduit diameter in conifer tracheids and angiosperm vessels. Data points are mean values for different species or organs; vessel data from stems only. Regression slopes (reduced major axis) were 2.38 in conifers and 1.85 in angiosperms and not different ( $P > 0.05$ ) from the second-power scaling predicted for lumen conductivity from the Hagen–Poiseuille equation (solid diagonal). (B) Sapwood area conductivity (conductivity per sapwood area) vs. conduit diameter for same conifer and angiosperm wood samples as in (A).

efficiency for a fixed tracheid length in each species or organ sampled. A tracheid length constraint is understandable because tracheids grow only a few percentage points longer than their fusiform initials (Bailey, 1920). It is apparent, however, that this length constraint is not simply an upper limit imposed by unicellularity because it varies considerably between species and organs. Furthermore, unicellular tracheids in other groups like ferns can achieve much greater lengths than the maximum in conifers (Veres, 1990). The need to maintain wood strength may contribute to a species- or organ-specific limit on tracheid length as discussed in a later section.

Although multicellular vessels achieve much greater lengths than unicellular tracheids, their substantial end-wall resistivity suggests that they have still encountered some kind of length limitation—just at much longer lengths than for tracheids. Their  $56 \pm 2\%$  end-wall contribution is less than the 67% optimum predicted for the fixed length scenario (Fig. 4A, open circle on dashed curve), but still comes close to maximizing

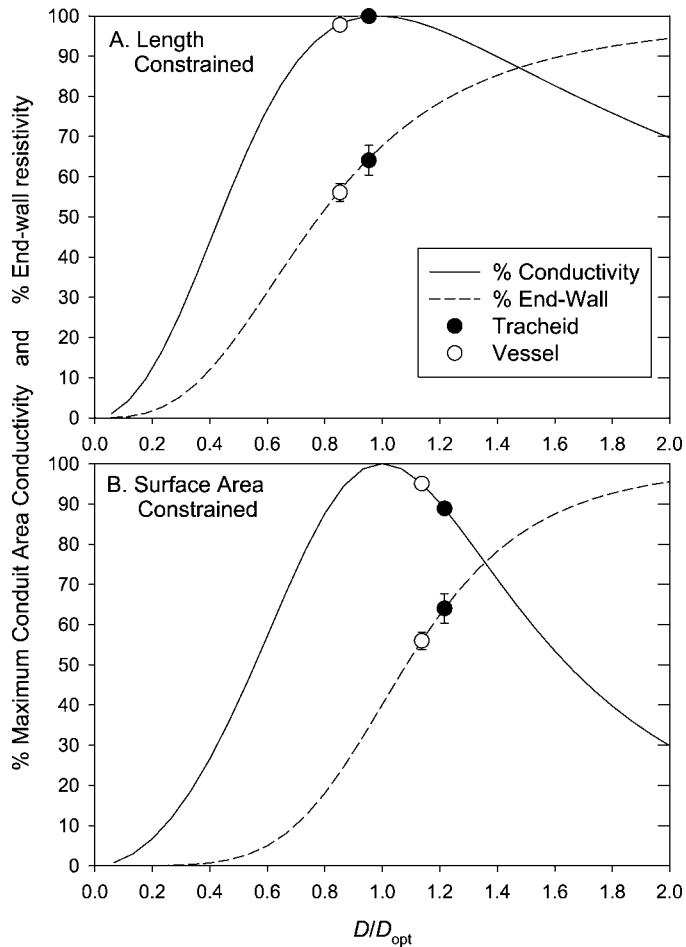


Fig. 4. Conduit-area conductivity (conductivity per lumen area, solid curve) and percentage of conduit resistivity in the end-wall (dashed curve) vs. conduit diameter for a conduit of constant length (A) or constant surface area (B). There is an optimal diameter ( $D_{opt}$ ) that maximizes the conduit area conductivity for each of the two size constraints. When length is constrained (A), maximum conductivity occurs when the end-walls contribute 67% of the total flow resistivity. When surface area is constrained (B) conductivity is maximized at 40% end-wall resistivity. Symbols show the 64% end-wall average for conifer tracheids and the 56% average for angiosperm vessels, along with the corresponding conduit area conductivity. Data from Pittermann et al. (2006b) and Hacke et al. (2006).

vessel area conductivity because of the broad optimum (open circle on solid curve). Unlike tracheids, vessels have no simple developmental limit on length, because it depends only on how many vessel elements can be lined up. Functional limits may be more important. Longer vessels cause a greater drop in hydraulic conductance when they fail and reduce the maximum carrying capacity of the xylem (Comstock and Sperry, 2000). Length may also indirectly be limited by a constraint on vessel surface area as discussed below in relation to cavitation protection. If the optimization exercise in Fig. 4A is repeated for a constant vessel surface area instead of constant length, the maximum conduit area conductivity occurs at 40% end-wall resistivity instead of 67% (Fig. 4B, Fig. 2, 40% diagonal). Vessels are intermediate between these two scenarios, but either way, the data indicate a species-specific constraint on vessel size.

## HYDRAULIC SIGNIFICANCE OF THE TORUS-MARGO PIT MEMBRANE

There is a paradox in the data presented in Figs. 1–3. Figure 1 shows that vessels have a much higher length-to-diameter ratio (average  $1660 \pm 180$ ) than tracheids (average  $104 \pm 5.9$ ). Yet Fig. 2 indicates that both conduit types have very similar end-wall bottlenecks to xylem flow, and Fig. 3 shows that as a result of this, tracheids and vessels have similar conduit area conductivities for the same diameter. How can vessels be 10 times longer than a tracheid of the same diameter and yet experience essentially the same end-wall bottleneck and conductivity? Seemingly, the only answer is that conifer tracheids must have much higher pit conductance per tracheid wall area than vessels to compensate for the much greater number of end-walls crossed per unit length.

We have recently estimated that the higher pit area conductance per tracheid wall area is achieved by a 59-fold higher conductance of conifer pits per pit area as compared to angiosperms (Pittermann et al., 2005). Based on earlier calculations, we attributed this higher conductance to the torus-margo pit membrane structure (Hacke et al., 2004). This membrane permits large pores to maximize water flow in the margo region without compromising the ability of the pit to seal off an air–water interface to protect against the air-seeding of cavitation. The sealing function of the pit is performed by the aspiration of the impermeable torus. In contrast, the typical intervessel pit membrane must have much narrower pores because without a torus the pit must be sealed against air-seeding by capillary forces alone.

The superior hydraulic conductance through the torus-margo membrane compensates for the much shorter length of tracheids, thereby minimizing the difference in hydraulic efficiency between conifers and angiosperms. The homoxyloous xylem of conifers also plays a role by packing more tracheids per unit sapwood area than the dispersed vessels of heteroxyloous angiosperms. When conducting efficiency is expressed on a sapwood area basis rather than on a conduit area basis, conifers actually average greater sapwood conductivity per area than angiosperms for the same conduit diameter (Fig. 3B).

Apparently, the angiosperms evolved longer conduits instead of sophisticated pits like conifers. Vessels are approximately 7.7-fold longer than tracheids of the same diameter: just long enough for vessels to compensate for their seemingly inferior pits and achieve a similar conductivity for the same girth (Pittermann et al., 2005). The great length of vessels in some species corresponds with diameters much wider than the widest tracheid. The ability of vessels to reach greater length and diameter than tracheids allows them to overcome the disadvantages of their pits and their dispersed vessel arrangement, thereby allowing at least some species to achieve greater maximum sapwood area conductivity than conifers—although the two wood types overlap considerably in this parameter (Fig. 3B).

It is not known if the torus-margo membrane in conifers evolved once as suggested by the hypothetical phylogeny in Fig. 5. Structural variation in the membrane between conifer groups could indicate otherwise (Bauch et al., 1972). Although relationships between gymnosperm groups are problematic, recent work suggests they are monophyletic with cycads at the base (Fig. 5, Burleigh and Matthews, 2004). The torus-margo structure might have evolved after the cycad split, thereby

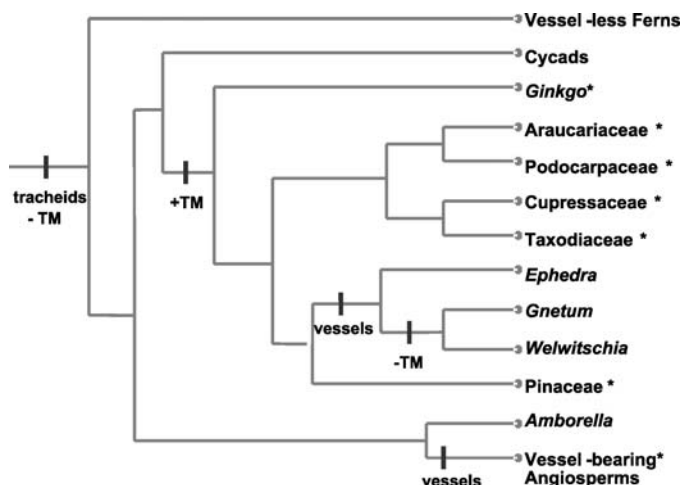


Fig. 5. Hypothetical relationships of relevant taxa (Burleigh and Matthews, 2004) showing possible points of origin and loss of the gymnosperm torus-margo pit membrane ( $\pm$  TM) and the origin of vessels in gymnosperms and angiosperms. Groups studied are asterisked. Branch lengths have no significance.

improving conducting efficiency. The ancestral condition—tracheid-based secondary xylem with homogenous pit membranes—is presumably approximated in extant plants by the secondary xylem of cycads and the basal vessel-less angiosperm *Amborella trichopoda* Baill. (Fig. 5). This ancestral wood ought to have had relatively low conducting efficiency because of the combination of short conduits and high-resistance pit membranes. Whether this condition persists in the cycads and vessel-less angiosperms is unknown. Sapwood area conductivities in vessel-less angiosperms are low, but not that different from conifer wood (Feild et al., 2000), suggesting that modifications have occurred to improve the conductivity of the pit membranes linking angiosperm tracheids—possibly increased porosity as observed in *Amborella trichopoda* (Feild et al., 2000) and *Tetracentron sinense* (Carlquist, 1992).

If the torus-margo pit membrane is hydraulically superior to the homogenous membrane, it should be beneficial to vessels as well as tracheids. In fact, some derived angiosperms have a seemingly analogous torus (Wheeler, 1983; Jansen et al., 2004). Vessels with torus-margo pitting have also evolved within the gymnosperms as indicated by the apparently basal Gnetophyte genus *Ephedra* (Fig. 5, Carlquist, 1996). However, there are also indications that a torus-margo structure may not be universally advantageous. In conifers with a distinct torus-margo membrane in earlywood tracheids, pits in latewood tend to have a less distinct organization (Liese, 1965; Petty and Puritch, 1970; Petty, 1972; Domec and Gartner, 2002a). In angiosperms that have an analogous torus structure, it tends to be limited to narrower vessels (Jansen et al., 2004). In the vessel-bearing the Gnetophyte genus *Gnetum*, some species have retained the torus-margo structure while other species have reverted to a homogenous pit membrane (Carlquist, 1996). A possible disadvantage of the torus-margo membrane is that once the torus is aspirated it can become stuck, permanently closing down flow even if embolized tracheids can be refilled (Siau, 1984; Sperry and Tyree, 1990). In contrast, refilled vessels with homogenous pits can readily regain their original flow capacity (Sperry et al., 1988).

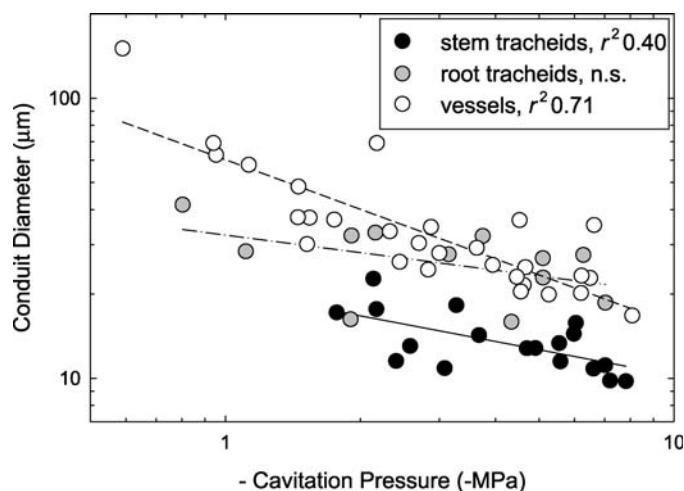


Fig. 6. The complex relationship between cavitation pressure and conduit diameter. Data points are mean values for different species or organs; vessel data from stems only. Separate trends exist in angiosperm stem vessels and conifer stem tracheids for narrower diameters to have greater protection from cavitation. There was no significant relationship for conifer root tracheids. Data from Pittermann et al. (2006a) and Hacke et al. (2006).

## CONDUIT SIZE AND CAVITATION

The previous sections emphasize the greater developmental limitation on unicellular tracheid size vs. larger multicellular vessels and the consequences for hydraulic efficiency. The data suggest that for a species or organ, conduit shape maximizes conducting efficiency given a constraint on conduit length or surface area (Figs. 1–4). But what results in this tracheid or vessel size limit being larger in some species than others? In this section we consider how conduit size might be limited by the need to protect against cavitation—the rapid growth of the vapor phase in a water-filled conduit. Species or organs that need less protection from cavitation may be able to exploit the greater conducting efficiency of larger conduits.

Based in part on correlations between habitat and conduit diameter, it has long been suspected that wider conduits are more vulnerable to cavitation (Carlquist, 1975; Baas, 1986). With respect to cavitation caused by freeze-thaw cycles, this has been confirmed by experiment and it is consistent with proposed cavitation mechanisms, although more remains to be learned (Ewers, 1985; Cochard and Tyree, 1990; Lo Gullo and Salleo, 1993; Davis et al., 1999; Pittermann and Sperry, 2003; Cavender-Bares, 2005). The situation is more complex for cavitation caused by water stress (Tyree et al., 1994).

The complexity is evident by comparing cavitation pressure of a xylem sample with its representative conduit diameter (Fig. 6). Cavitation pressure of the xylem sap is represented by either the mean cavitation pressure (angiosperm data) or the pressure causing a 50% loss of conductivity ( $P_{50}$ , conifer data). The two metrics are similar for the typically sigmoidal relationship between conductivity and xylem pressure in conifers and many angiosperms. There is no simple relationship between conduit diameter and cavitation pressure across tracheids and vessels. As has been known for some time (Tyree and Sperry, 1989), conifer tracheids show the same wide range in cavitation pressure as angiosperm vessels despite their narrower diameter range and much shorter lengths.

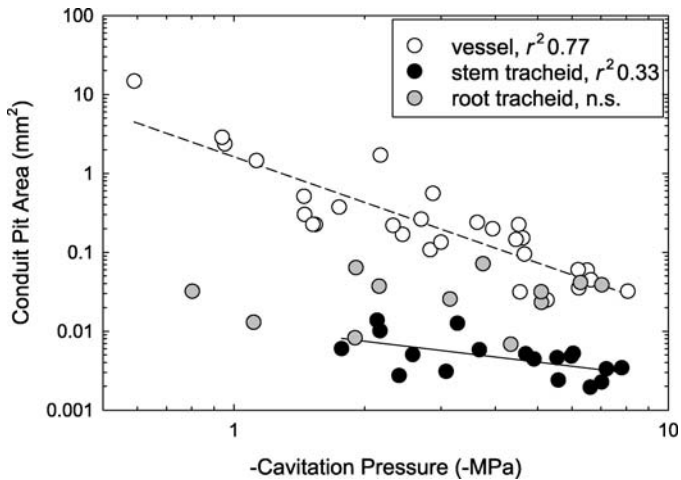


Fig. 7. The relationship between cavitation pressure and inter-conduit pit area per conduit. Data points are mean values for different species or organs; vessel data from stems only. Greater resistance to cavitation in angiosperm vessels corresponds to a smaller area of inter-conduit pits. According to the “pit area hypothesis” this is a causal relationship. No consistent relationship occurs for conifer tracheids, which have a very different torus-margo mode of pit function. Data from Pittermann et al. (2006b), Hacke et al. (2006).

Within both angiosperms and conifers, species with narrower stem conduits were more resistant to cavitation on average (Fig. 6). Conifer stem tracheids were more vulnerable for their diameter, however, than angiosperm vessels. Conifer root tracheids showed no diameter vs. vulnerability relationship, but were generally wider for a given cavitation pressure than stem tracheids (Fig. 6, gray symbols). The diameter-vulnerability trends are statistically noisy and not always observed in other data sets, depending on the number and kinds of species compared (Cochard, 1992; Tyree et al., 1994; Pockman and Sperry, 2000). The data in Fig. 6 show significant trends only because of the very wide range in cavitation pressure. Had we sampled just between 2 and 4 MPa, for example, trends would have been obscured. Clearly, any link between diameter and vulnerability is indirect.

The complexity is consistent with what is known about the mechanism of cavitation by water stress. Numerous experiments indicate that the cavitation by water stress is triggered by air entry into the xylem conduits (Sperry and Tyree, 1990; Cochard et al., 1992; Jarbeau et al., 1995; Sperry et al., 1996). The air-bubble “seeds” the expansion of the vapor phase, causing cavitation. An important site of air-seeding is the interconduit pits. While other air-seeding sites may be present, none have been identified. There is no self-evident reason why the air-seeding pressure of a conduit should be directly determined by conduit size, consistent with the complexity of diameter vs. vulnerability relationships.

We have recently advanced the “pit area hypothesis” to provide an indirect link between vessel size in angiosperms and vulnerability to cavitation (Wheeler et al., 2005). The hypothesis is based on a relatively tight correlation between the total intervessel pit area in a vessel and the cavitation pressure (Fig. 7,  $r^2 = 0.77$ ). The hypothesis is that this is a causal relationship. If cavitation occurs by air-seeding through pit membrane pores, the ease of air-seeding will be determined by the single largest membrane pore in contact with an air-

filled conduit. The more pit membrane area there is in a vessel, by chance the greater will be this largest membrane pore. By analogy, the more links there are in a chain, by chance the weaker it becomes. The same argument could be advanced if air-seeding occurred through the thick secondary wall of the vessel, except that in this case vessel surface area might show a tighter correlation with cavitation pressure than pit membrane area. This was not observed (Wheeler et al., 2005).

The pit area hypothesis has several corollary predictions. First is that average pit membrane porosity should be rather generic, not differing significantly on average across species. Otherwise, the relationship between total pit area of a vessel and the cavitation pressure (set by the largest membrane pore in the vessel) would not be as consistent as we observed. Carrying on with the chain analogy, if the strength of different chains is to be determined by the number of their links, all links must be made after the same basic pattern in all chains. In support of this, there was no correlation between the estimated flow resistance through vessel pits and cavitation pressure (Wheeler et al., 2005). This suggests that the average pit membrane porosity does not vary systematically with cavitation pressure. This finding contradicted the possibility that species with greater resistance to cavitation should have less porous pit membranes and higher membrane flow resistances on average (Sperry and Hacke, 2004).

A second corollary is that the fraction of the vessel surface area that is occupied by intervessel pits should be quite small. This will maximize vessel size for a given safety from cavitation, and minimize the trade-off between cavitation protection and vessel size plus conducting efficiency. The measured fraction is small, with intervessel pits occupying on average only  $6 \pm 1\%$  of the vessel wall surface area (Hacke et al., 2006). Note that this percentage reflects only the intervessel pitting, not the often abundant vessel-to-parenchyma pitting, which according to the hypothesis, is not an air-seeding liability.

A third prediction is that vessel shape and percentage of end-wall resistivity should result in the maximum vessel area conductivity for a given vessel surface area. According to the pit area hypothesis, the vessel surface area is constrained by the need to have a minimum surface of intervessel pitting for cavitation protection, and by the advantage of a low pit area percentage. As discussed, the  $56 \pm 2\%$  end-wall resistivity places vessels in between the optima for constrained surface area and constrained length (Fig. 4).

A final corollary is that the pit area hypothesis should be able to explain the variable relationship between vessel diameter and vulnerability to cavitation. This is explained in part by variation in the percentage of wall area occupied by intervessel pits. Although this averaged 6%, it ranged from 0.4 to 21% (Hacke et al., 2006). For a given pit membrane area and cavitation pressure, a pit fraction of 0.4% would correspond to a relatively wide and long vessel with high conductivity, whereas a pit fraction of 21% will result in a relatively narrow and short vessel with low conductivity. Both sizes would have identical vulnerability to drought-induced cavitation. Another source of variation is in the relationship between vessel pit area and cavitation pressure (Fig. 7, vessels). While some of this may be measurement error, some is probably also because of structural variation in pit membranes across the angiosperms—variations on the “generic” membrane structure of intervessel pits.

Does the pit area hypothesis apply to conifers? The data

suggest that it does not. Although stem tracheids show a relationship between tracheid pit area and cavitation pressure, root tracheids do not, nor do all tracheids pooled (Fig. 7, tracheids). It is possible that the significant relationship in stem tracheids is simply the consequence of fewer pits fitting into tracheids that become smaller with increasing cavitation protection for some other reason. Given the very different torus-margo structure and function of the conifer pit membrane, it is not surprising that the pit area hypothesis is not supported.

Air-seeding in the torus-margo pits of conifer early-wood tracheids is thought to occur when the torus is displaced from its sealing position by stretching and possible rupturing of the margo (Sperry and Tyree, 1990). The differences in air-seeding pressure between species are predicted to be a function of the number of margo strands holding the torus in place and their mechanical properties (Hacke et al., 2004). This is consistent with observations of more robust margo structure in tracheids that are more resistant to cavitation (Sperry and Tyree, 1990). It is also consistent with an increase in pit membrane flow resistance with cavitation protection in tracheids of north-temperate conifers, indicating a trend to a less porous margo with greater resistance to air-seeding (Pittermann et al., 2006a). Rather than air-seeding depending on the amount of “generic” pit membrane present as in angiosperm vessels, it may be controlled by adaptive differences in individual pit structure between species. This is as if the strength of different chains is being controlled by variation in link design rather than simply the number of links made off the same pattern.

If the cavitation pressure of a tracheid is not significantly influenced by the quantity of pitting, and if the main site of air-seeding is at the pits, there is no obvious rationale for a linkage between the protection against air-seeding and the size of a tracheid (Pittermann et al., 2006a). In theory, the largest of tracheids could occur in combination with air-tight end-walls for maximum protection from cavitation. Nevertheless, wider tracheids were more vulnerable, at least within stems (Fig. 6). We conclude that some other factor must result in the relationship between tracheid size and cavitation protection.

#### CONDUIT SIZE AND MECHANICAL STRENGTH

Xylem conduits, in addition to transporting water efficiently while avoiding cavitation, must also protect themselves against implosion. Negative sap pressure puts the conduit wall under compression, drawing it inward. Unless reinforced with lignin, cellulose walls cannot resist this compression. The evolution of thick and lignified walls was a prerequisite for transport under significant negative pressure (Raven, 1987). An additional threat of implosion comes from forces on the conduit wall from gravity, wind, and other mechanical challenges to the plant body. In the earliest vascular plants this added challenge was minimized because xylem conduits were located at the neutral axis of the stem center where bending forces are minimal (Speck and Vogellehner, 1988; Niklas, 1990; Vincent and Jeronimidis, 1991).

In contrast, the wood of conifers and angiosperms not only transports water but also holds up free-standing plants. In the homoxylous wood of conifers, the tracheid must be strong enough to hold open the water column and hold up the tree at the same time. In heteroxylous angiosperm wood, fibers take on much of the plant support task, relaxing this demand on

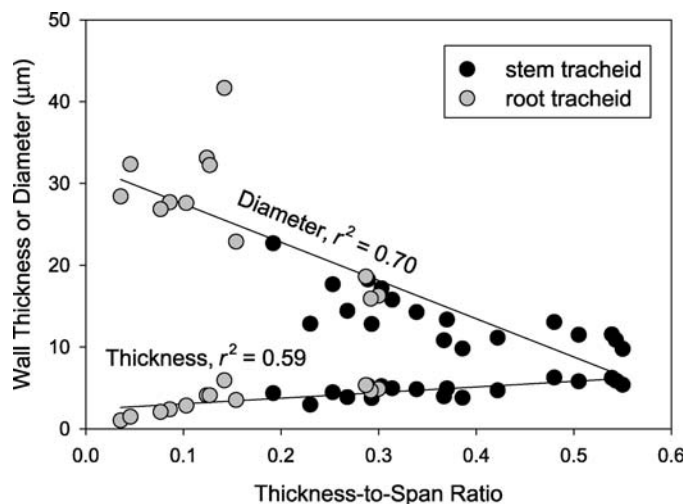


Fig. 8. Variation in thickness-to-span ratio ( $x$ -axis) in conifer tracheids is primarily a result of variation in tracheid diameter rather than wall thickness. Data points are mean values for different species or organs (from Pittermann et al., 2006a).

vessel strength. A priori we expect that any mechanical constraint on conduit size should be more limiting for conifer tracheids than angiosperm vessels.

The size of a conduit should have important consequences for its strength against implosion. To a first approximation, this strength is proportional to the “thickness-to-span” ratio of the conduit (Hacke et al., 2001)—the double-wall thickness per lumen diameter. This ratio correlates with collapse by negative pressure of fibers in *Eucalyptus* wood (Bisset and Ellwood, 1951) as well as the collapse of fibers during paper making (Lundgren, 2004). Wall thickness per lumen diameter is a major determinant of wood density, which correlates strongly with a variety of wood mechanical properties (Panshin and de Zeeuw, 1970). If conduit strength is to be independent of conduit size, the wall thickness must increase in proportion to the conduit diameter.

It follows that any limit to wall thickness can lead to a mechanical constraint on conduit diameter. To maximize lumen diameter and conducting efficiency for a given mechanical strength, the conduit walls should be as thick as possible. “As thick as possible” would be determined by the rate and duration of wall growth before the conduit must die to become functional. If walls are always near their maximum thickness, the conduit can only achieve greater strength against implosion by narrowing its diameter. If this is happening, wall thickness should vary much less across conduit size and strength than diameter.

This mechanical constraint may play a preeminent role in limiting tracheid sizes in the homoxylous wood of conifers. Two observations support this idea. First, variation in thickness-to-span ratio across the conifer data set was overwhelmingly determined by diameter rather than wall thickness (Fig. 8, Pittermann et al., 2006b). This is consistent with wall thickness being near a developmental maximum across the board, requiring greater strength to be achieved by narrowing diameter. Second, stem tracheids were narrower than root tracheids, yet had similar wall thickness (Fig. 8). Stem tracheids presumably must be stronger against implosion than root tracheids because they have the additional burden of

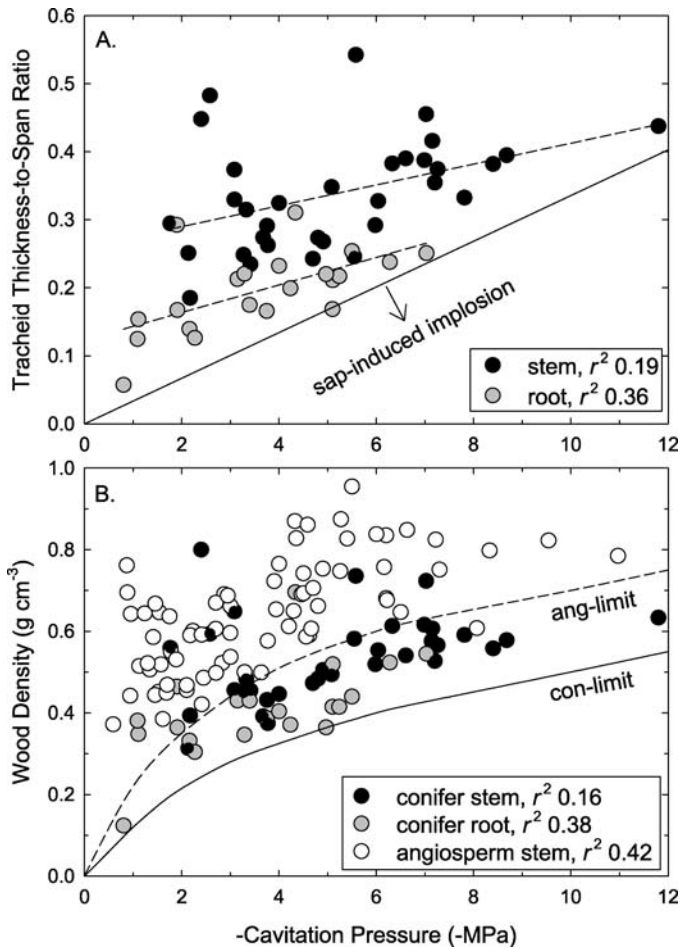


Fig. 9. Mechanical strength parameters in relation to cavitation resistance. (A) Tracheid thickness-to-span ratio (y-axis) tends to increase with greater protection from cavitation (cavitation pressure, x-axis). The diagonal is a conceptual limit below which negative sap pressure could threaten to implode a tracheid. (B) Wood density, a nonlinear correlate of thickness-to-span ratio, also tends to increase with greater cavitation protection. The conceptual implosion limit is shown as a curve. Separate limits appear to apply to conifer (con-limit) and angiosperm wood (ang-limit). Data from Pittermann et al. (2006b), Hacke et al. (2006), and unpublished wood density values accompanying the cavitation pressures in Wheeler et al. (2005) and Hacke et al. (2006). Data points are mean values for different species or organs; angiosperm data from stems only.

holding up the foliage. Because the ability to gain strength by increasing wall thickness is limited, they must become narrower instead.

A mechanical constraint on tracheid diameter can also explain why narrow tracheids and protection from cavitation tend to go together (Fig. 6, Pittermann et al., 2006b). Greater protection from cavitation is associated with more arid habitats and lower negative sap pressures (Pockman and Sperry, 2000). More negative sap pressures require stronger tracheids with greater thickness-to-span to resist implosion (Fig. 9A, additional data from Hacke et al., 2004). Greater thickness-to-span means narrower diameter (Fig. 8) because walls are presumably as thick as possible. Root tracheids can be weaker and wider than stem tracheids for the same cavitation pressure (Figs. 6, 9A) because they do not need as much extra reinforcement to resist bending of the axis.

According to this interpretation, the diameter-vulnerability relationship in tracheids (Fig. 6) is not required to protect against air-seeding and cavitation per se, but rather to withstand implosion by more negative sap pressure. The tendency for tracheid thickness-to-span to increase with more negative cavitation pressure is consistent with a tendency for conifer wood density to increase (Fig. 9B, conifer data: Hacke et al., 2001).

Variation in the tracheid diameter vs. vulnerability link (Fig. 6) is consistent with variation in the thickness-to-span and density vs. vulnerability relationships (Fig. 9AB). Negative sap pressure is only one of many possible demands on thickness-to-span ratio and wood density. The “sap-induced implosion” diagonal in Fig. 9A is a conceptual lower limit: the minimum thickness-to-span ratio required to avoid implosion by sap pressure. Its analogue for the density relationship is shown as the “con-limit” curve in Fig. 9B. As mentioned, roots are less mechanically challenged by bending than stems and come closer to this limit. But some data points, mostly stems, are quite far above the minimum strength boundary. This may reflect additional demands beyond that of negative sap pressure. Windy or snowy habitats may require greater resistance to branch breakage (Mayr et al., in press). Greater wood density might promote slow growth and longevity of woody parts—adaptive traits in nutrient-limited habitats (King, 1993). Extra stiffness could be necessary to efficiently support horizontal branches in some architectures. The most extreme data points, in the upper left corner of each panel, are from Podocarpaceae and Araucariaceae species (Pittermann et al., 2006b). Their exceptional density and thickness-to-span at modest cavitation pressure may result from selection for longevity in their typically wet and sometimes nutrient-poor habitats.

Tracheid diameter co-varies with wood strength parameters, but it also co-varies with tracheid length to maximize conducting efficiency (Fig. 4A). Interpreting the cause-and-effect behind these two correlations is complicated. The fact that diameters are so close to the hydraulic optimum for a fixed length suggests that length is the ultimate constraint on diameter, with a strength requirement perhaps driving the variation in lengths between species and organs. Tracheid length may also be important for wood strength even independent of its association with a narrower optimal diameter (Panshin and de Zeeuw, 1970), although this is difficult to know because the two dimensions scale so closely (Fig. 1).

In contrast to tracheids, vessel size may be most directly constrained by the need to protect against cavitation by air-seeding (via the pit area hypothesis, Wheeler et al., 2005) and only secondarily, if at all, limited by mechanical constraints. With fibers to bear additional stress, vessel walls need only withstand implosion by negative pressure. Accordingly, vessels tend to have smaller thickness-to-span at their intervessel walls than even the root tracheids of conifers (Sperry and Hacke, 2004). In addition, fibers can surround vessel clusters and probably help prop vessels open, making vessel wall thickness less critical. Both factors would allow much wider lumen diameters for the same safety from implosion by negative pressure than in conifer tracheids.

The importance of fibers for bolstering vessel strength is suggested by an increase in angiosperm wood density with cavitation protection—the same trend seen in conifers (Fig. 9B, open symbols). The angiosperm data come from Sperry and Hacke (2004), plus unpublished wood density measurements



that accompany the cavitation pressures reported in Hacke et al. (2006) and Wheeler et al. (2005). Angiosperm wood tends to be denser for a given cavitation pressure than conifer wood because of its sizable fraction of fibers (Fig. 9B), and the conceptual minimum density required to support a given cavitation pressure is greater (dashed “ang-limit” curve in Fig. 9B). The increase in angiosperm wood density with cavitation resistance results from the combination of two factors: an increase in the volume fraction of wood devoted to fibers (Hacke et al., 2006), and an increase in fiber thickness-to-span ratio (Jacobsen et al., 2005). Just as in the conifer situation, there is considerable variation in angiosperm wood density above the boundary line that is not related to cavitation pressure and may reflect additional functions for high wood density.

## ECOLOGICAL AND EVOLUTIONARY IMPLICATIONS

The size–function relationships shown in the figures are empirical, but the constraints driving their evolution are a matter of interpretation. Interpretations must be tested and refined. Although the proposed trade-offs are hypothetical, it is useful to consider their implications for trends in ecological and evolutionary wood anatomy.

Under what ecological circumstances might the transport properties of conifer tracheids be superior to angiosperm vessels? The conducting efficiency of conifer wood on a sapwood-area basis actually exceeds that of angiosperm wood for the same conduit diameter, thanks to the combination of torus-margo pits and homoxylous organization (Fig. 3B). Any factor that limits vessel diameter to within the tracheid range should therefore favor conifer water transport. Water-limited habitats are such a factor, because according to the pit area hypothesis, vessels must be small to minimize cavitation. For cavitation pressures below  $-2$  MPa, there is overlap in sapwood area conductivity of conifer and angiosperm branch wood (data not shown).

Habitats where freezing occurs during the growing season can also limit vessel diameters to within the tracheid range. Experimental work suggests that mean vessel and tracheid sizes need to be less than  $30\ \mu\text{m}$  to avoid cavitation by freezing and thawing (Pittermann and Sperry, 2003). While  $30\ \mu\text{m}$  is a respectable diameter for a tracheid, it is a relatively narrow vessel. The many tracheids narrower than the cavitation threshold are ready to function when transpiration resumes early in the spring (Pittermann and Sperry, 2006). These limits to vessel size caused by water and freezing stress are consistent with conifers being an important element of north temperate arid and boreal ecosystems.

Another advantage of conifers in water- or nutrient-limited habitats is that their homoxylous wood can be less dense for the same cavitation pressure than the fiber-containing wood of angiosperms (Fig. 9B). Conifers should be able to grow larger for the same biomass and negative pressure requirement than angiosperms, an advantage in resource-limited habitats. And finally, many conifers maintain large margins of safety from drought-induced cavitation—particularly in their stem xylem (Pinol and Sala, 2000; Hubbard et al., 2001). We attribute this to the lack of any strong trade-off between tracheid size and protection against air-seeding. The luxury of a large safety margin may contribute to the longevity of some conifers, which

can be advantageous in nutrient- or water-limited sites (King, 1993).

It may also be true that greater conducting efficiency is not equally advantageous in all circumstances. More efficient xylem can transport water at a higher rate for the same cross-sectional area and pressure drop. It may be most important in habitats with potentially high transpiration rates and greater competition for water. It would be less important in humid, wet, or low-light habitats, or where nutrients are more limiting than water. These conditions would minimize the importance of trade-offs between conducting efficiency and competing functions. Some Podocarpaceae and Araucariaceae species that we sampled grow in such habitats, and it is possible that any disadvantage of their dense and therefore hydraulically inefficient wood is offset by the advantage of dense wood for the promotion of longevity and slow growth rate—factors that contribute to their persistence in rain and cloud forests of the south-temperate zone (Pittermann et al., 2006b). Ecological and functional wood anatomy would profit from a cost-benefit analysis of conducting efficiency across a spectrum of ecological contexts.

Turning to evolution, the ancestral vascular type was tracheid-based without secondary growth (Raven, 1987). The tracheids were not significantly involved in supporting the plant body. This describes the primary xylem of a variety of extant plants, including the vessel-less ferns (Fig. 5). Free of any mechanical burden aside from resisting implosion by sap pressure, these primitive tracheids were potentially free to reach larger sizes than their descendants in conifer wood (Niklas, 1985). Fern tracheids, for example, reach centimeters in length and over  $80\ \mu\text{m}$  in diameter (Veres, 1990). As a consequence, their conducting efficiency could be relatively high, even if their pits lacked the hydraulic efficiency of a torus-margo organization. The evolution of longer and wider vessels from these tracheids created no problem for support of the plant body because the tracheids were not structurally important to begin with (Vincent and Jeronimidis, 1991). Consistent with this, there is a relatively high incidence of independent vessel evolution in ferns (Carlquist and Schneider, 1999).

The evolution of secondary xylem enabled plants to grow taller, but brought with it the problem of combining mechanical support and vascular function in one tissue. Assuming that ancestral wood was homoxylous, mechanical constraints may have forced a reduction in tracheid size well below that of the primary xylem. Conducting efficiency would be extremely low, combining the disadvantages of short and narrow tracheids with possibly high-resistance, unspecialized pit membranes. The evolution of the torus-margo pit membrane would have solved a major problem—permitting an order-of-magnitude leap in conducting efficiency (Pittermann et al., 2005) without compromising the mechanical role of the tracheids in homoxylous wood.

The alternative solution in the angiosperm lineage was the evolution of heteroxylous wood with vessels. The literature has emphasized the significance of the origin of vessels themselves (Cronquist, 1988). But much more may have been required for vessels to fulfill their hydraulic potential in secondary xylem. It is not enough for tracheid end-walls to become perforation plates, because as long as the wood remained homoxylous, conduit diameters could not increase beyond the same mechanical limits that we suggest limit the size of conifer tracheids. The end-wall resistivity would be reduced, but

possibly at the price of increased vulnerability to cavitation. According to the pit-area hypothesis, the opening of tracheid end-walls could increase the total area of homogenous pits in the conduit, increasing the vulnerability to air-seeding.

The evolution of vessels in angiosperm wood may have faced problems of mechanical and hydraulic stability—problems solved only by the evolution of a fiber matrix and the heteroxylous condition. Fibers were essential for taking on the mechanical role of the homoxylous conduit and freeing it to achieve greater size. Presumably the vessel network also had to evolve to minimize the pit-contact area and vulnerability to cavitation. The coordination of these evolutionary changes may have required a reduction in plant stature and water stress, relaxing the mechanical and hydraulic demands while the heteroxylous condition originated. Perhaps the herbaceous and aquatic groups at the base of the angiosperm tree arose at this phase (Soltis and Soltis, 2004), along with a number of basal vines and lianas—mechanical parasites (Feild and Arens, 2005). More study of xylem function in transitional groups will shed light on the problems facing vessel evolution in angiosperms.

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