



## Review

# Hydraulic safety margins and embolism reversal in stems and leaves: Why are conifers and angiosperms so different?

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## ABSTRACT

Angiosperm and coniferous tree species utilize a continuum of hydraulic strategies. Hydraulic safety margins (defined as differences between naturally occurring xylem pressures and pressures that would cause hydraulic dysfunction, or differences between pressures resulting in loss of hydraulic function in adjacent organs (e.g., stems vs. leaves) tend to be much greater in conifers than angiosperms and serve to prevent stem embolism. However, conifers tend to experience embolism more frequently in leaves and roots than angiosperms. Embolism repair is thought to occur by active transport of sugars into empty conduits followed by passive water movement. The most likely source of sugar for refilling is from nonstructural carbohydrate depolymerization in nearby parenchyma cells. Compared to angiosperms, conifers tend to have little parenchyma or nonstructural carbohydrates in their wood. The ability to rapidly repair embolisms may rely on having nearby parenchyma cells, which could explain the need for greater safety margins in conifer wood as compared to angiosperms. The frequent embolisms that occur in the distal portions of conifers are readily repaired, perhaps due to the abundant parenchyma in leaves and roots, and these distal tissues may act as hydraulic circuit breakers that prevent tension-induced embolisms in the attached stems. Frequent embolisms in conifer leaves may also be due to weaker stomatal response to changes in ambient humidity. Although there is a continuum of hydraulic strategies among woody plants, there appear to be two distinct 'behaviors' at the extremes: (1) embolism prevention and (2) embolism occurrence and subsequent repair.

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## 1. Introduction

It has been nearly three decades since Zimmermann [1] proposed the hydraulic segmentation hypothesis, which was later modified by Tyree and Ewers [2] as the hydraulic vulnerability segmentation hypothesis. Vulnerability in this context refers to the susceptibility to disruption of xylem water transport resulting from

its blockage by air embolisms. These classic hypotheses stipulate that distal portions of the hydraulic pathway should be more disposable than the stems to which they are attached enabling the more proximal stems to become hydraulically isolated when conditions warrant. In Zimmermann's version the segmentation is the result of the drop in water potential along the hydraulic continuum across segments with similar vulnerability to embolism. Tyree and Ewers made the additional stipulation of lower resistance to embolism in the distal segments that insure the safety of the more proximal stems. These views have guided much hydraulic research and how we view the plant hydraulic continuum. Although the

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idea that terminal components of the hydraulic pathway (roots and leaves) in which the plants have invested less energy should experience more embolism than stems is supported in many species [e.g., 3–6], it may only be part of the story of how plants cope with transpiration-induced negative pressures and resulting embolism in their xylem.

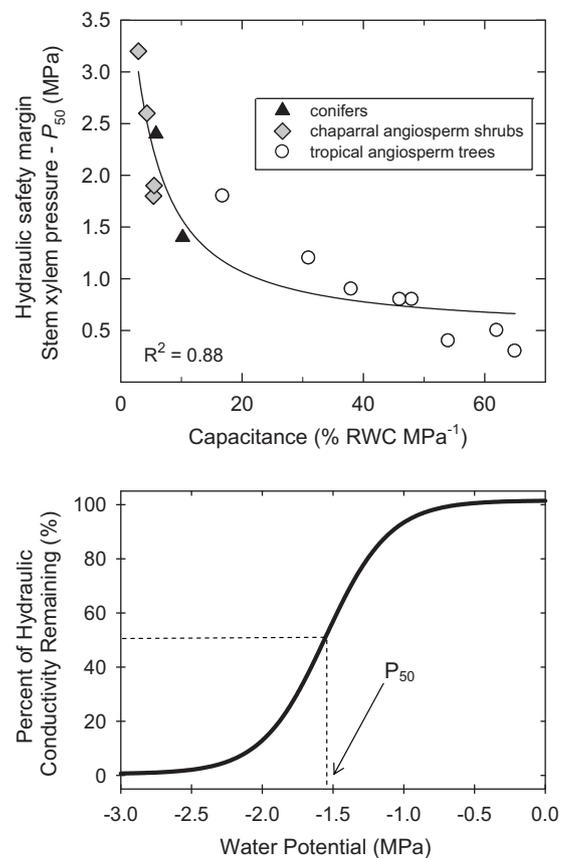
Embolism repair has received much attention lately [see 7–9]. The mechanism(s) responsible for embolism repair are still in question, but there is strong support that sugars are involved in the refilling process [10–13]. One other important question concerning embolism formation and repair is why do embolisms develop daily in different organs (roots, stems, leaves) of some species, but not in other species? What are the structural and physiological trade-offs involved in experiencing versus avoiding frequent embolism in a given plant organ? What are the costs and benefits associated with leaving stomata open permitting carbon fixation while allowing tension-induced xylem dysfunction to develop that subsequently needs to be repaired, versus constructing a xylem that is embolism resistant? Are there characteristics of species that embolize daily that allow them to be more efficient at embolism repair than species that avoid embolism? These will be the guiding questions that this paper will explore. The data presented in this paper were obtained from a broad literature search and the goal was to make the data collection as inclusive and thorough as possible.

## 2. Hydraulic safety

The various metrics used to describe the degree of conservatism in a plant's hydraulic strategies are typically expressed as hydraulic safety margins. For example, the difference between the minimum xylem pressure a stem experiences during a day or season and the pressure at which it would lose 50% of its hydraulic conductivity ( $P_{\text{STEM}} - P_{50}$ , see Fig. 1a) is a very informative measure. It tells how close a species operates hydraulically to the steepest point of its xylem vulnerability curve and therefore to potentially catastrophic embolism. Xylem vulnerability curves describe the relationship between water status (as xylem pressure) and the percentage of hydraulic function remaining as compared to the maximum. They are typically sigmoid in shape, with low percentages of hydraulic function lost at pressures near zero until a threshold negative pressure is reached at which air entry begins to accelerate. Once a tissue has reached its  $P_{50}$  it is on the part of the curve that is steepest, which means that even a slight drop in pressure will produce a substantial reduction in hydraulic function (Fig. 1b).

Other hydraulic safety margins relate to properties between different plant organs. Stem  $P_{50}$  minus leaf  $P_{50}$  ( $P_{50\text{STEM}} - P_{50\text{LEAF}}$ ) informs of the magnitude of the difference between leaf hydraulic safety and stem hydraulic safety. It has been suggested that a highly negative  $P_{50\text{STEM}} - P_{50\text{LEAF}}$  may imply that leaves are acting as hydraulic fuses by embolising before stem xylem, closing their stomata and effectively stopping transpiration, thereby preventing stems upstream from reaching embolism-inducing xylem pressures [14]. These distal organs typically have more living tissue than stems [15] and these living tissues could be involved with embolism repair (see below). Another noteworthy aspect of plant hydraulic safety is that woody tissues become increasingly resistant to embolism with increasing height, especially in very tall trees [e.g., 16,17]. However, this difference in embolism resistance with height is small compared to the differences in safety margins between conifers and angiosperms.

Although a  $P_{\text{STEM}} - P_{50}$  continuum exists among conifers and angiosperms, conifers tend to have greater safety margins. Similarly, evidence suggests absolute values of  $P_{50\text{STEM}} - P_{50\text{LEAF}}$  and  $P_{50\text{STEM}} - P_{50\text{ROOT}}$  are greater in conifers than angiosperms (Fig. 2, [18–21]). Furthermore, it seems that many angiosperm species



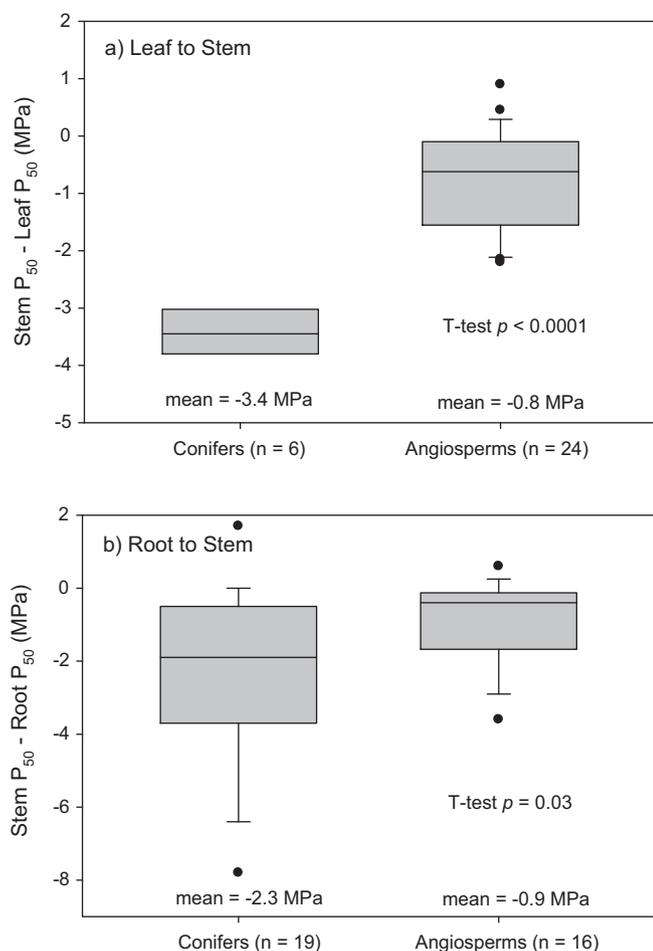
**Fig. 1.** Hydraulic safety margins decreased with increasing stem capacitance ((a), data from [26,72]) and a hypothetical vulnerability curve (b) illustrating that the  $P_{50}$  often occurs within the steepest portion of the curve.

are able to operate at negative safety margins (meaning that they would experience large amounts of embolism). Meinzer et al. [22] found that daily minimum water potentials in branches of tropical angiosperms corresponded to 24–40% losses in branch hydraulic conductivity. In fact, several studies have reported stem water potentials experienced during non-drought conditions resulting in daily losses of hydraulic conductivity in stems of tropical angiosperms [22–25]. There also appears to be a strong trade-off between hydraulic safety margins and stem hydraulic capacitance (Fig. 1a), such that species with high capacitance tend to have narrower (or even negative) safety margins [26]. Stem hydraulic capacitance is the amount of water released as stem xylem pressures become more negative. Capacitance contributes to embolism avoidance and therefore hydraulic safety through transient release of stored water into the transpiration stream, which buffers daily fluctuations in xylem pressure [26,27].

In order to achieve high intrinsic resistance to embolism (highly negative  $P_{50}$ ) in wood, species must construct a network of fibers and conduits with thick walls [28–30]. These investments in hydraulic safety result in wood that is very dense, but precludes having large volumes of living parenchyma cells, which may be a source of capacitance for embolism repair (see below).

## 3. Loss and recovery of hydraulic function

Loss and recovery of hydraulic conductance on a daily basis is more widespread in distal portions of the hydraulic pathway than in the main stem and branches due to lower resistance to embolism in roots and leaves as compared to stems [e.g., 5,18,19,31]. Conifers are particularly prone to loss and recovery of hydraulic conductance



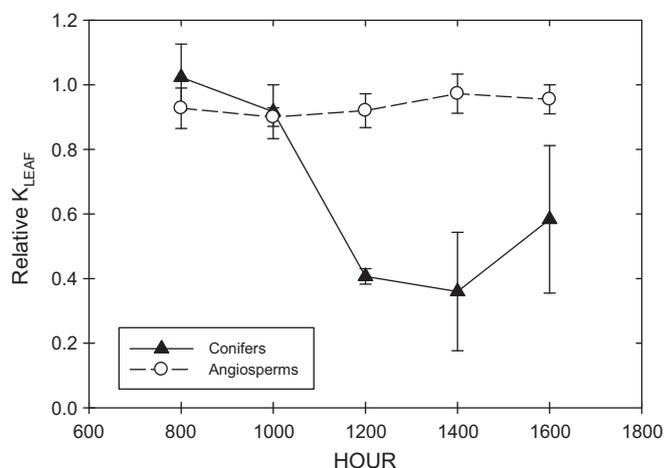
**Fig. 2.** Leaf to stem (a) and root to stem (b) safety margins are greater (more negative) in conifers than angiosperms. Boxes include the 25th to 75th percentiles, horizontal lines within boxes represent median values, horizontal lines outside of boxes represent 10th and 90th percentiles, and closed circles represent actual range of sampled measurements (data compiled from [18–22,25,31,32,73,5] and unpublished data on two conifer and two angiosperm species).

in leaves on a daily basis (Fig. 3, [21,32]), losing nearly 100% of their hydraulic conductance and restoring it completely by the next morning. However, loss and recovery of hydraulic function in angiosperm leaves has also been reported [33–36]. Loss and recovery of hydraulic function has been observed in roots of corn [37] and several tropical angiosperm tree species [38]. However, even stems of some species lose and recover hydraulic conductivity on a daily basis as has been shown in *Vitis* and multiple tree species [9,39–41], and this may be an especially common phenomenon in tropical tree species with low wood density [22].

An emerging picture is that a continuum of hydraulic safety strategies exists in conifers and angiosperms. However, conifers, in general, have large leaf-to-stem and root-to-stem safety margins. They experience little embolism in stems, but large degrees of embolism in distal tissues. Conversely, many angiosperms have very narrow or even negative safety margins and experience stem embolism and repair on a daily basis [22,24].

#### 4. Why are there differences between safety margins and loss and recovery of hydraulic capacity in angiosperms versus conifers?

Stomatal response to vapor pressure deficit (VPD) may be a major determinant of why species from different clades fall into



**Fig. 3.** Conifers but not angiosperms experienced loss and recovery in leaf hydraulic conductance ( $\blacktriangle$ , *Pinus virginiana*, *Pinus ponderosa* and *Pseudotsuga menziesii*) ( $\circ$  *Acer rubrum*, *Arbutus menziesii*, *Liriodendron tulipifera* and *Quercus garryana*). Lines indicate trends for each group; dashed represents the angiosperm species and solid represents the conifers. Data adapted from [21,32].

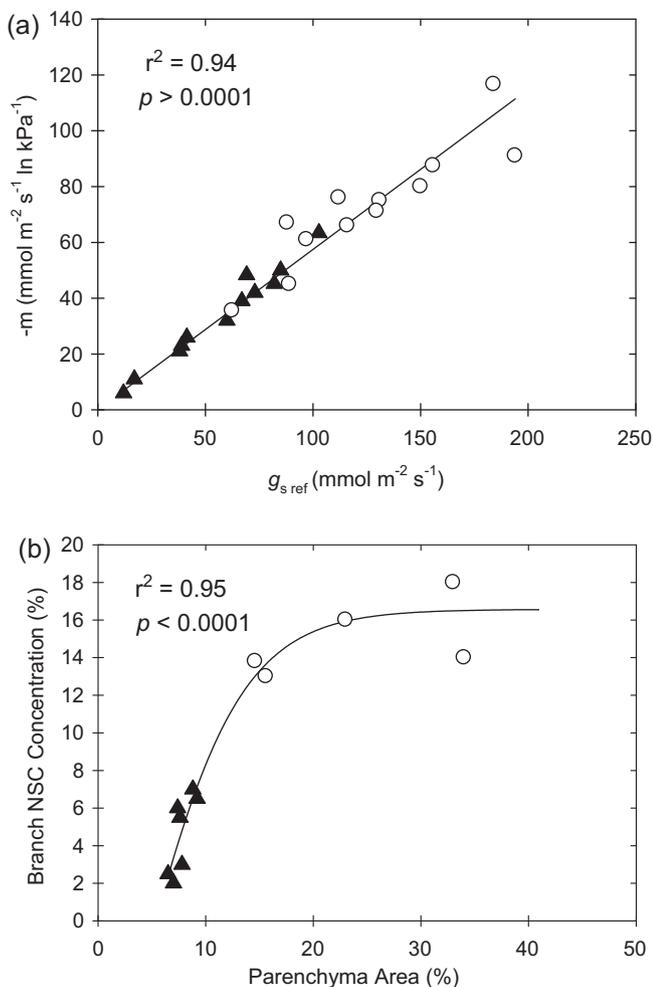
different hydraulic functional groups. Stomatal conductance ( $g_s$ ) generally declines with increasing VPD, but stomatal sensitivity to changes in VPD varies substantially across species [43–51]. A weaker stomatal response, either as sensitivity to VPD or response speed (i.e. kinetics), to reductions in humidity may represent a functional liability that necessitates mitigating strategies that prevent the development of excessive embolisms. These species may need to rely on “hydraulic circuit breakers”, such as highly vulnerable leaves to prevent stems from experiencing dangerous xylem pressures, while species with greater stomatal sensitivity can rely more on the stomatal response. Using an analysis adapted from [44] we compared stomatal sensitivity of angiosperms and conifers to VPD using the following equation:

$$g_s = -m \ln \text{VPD} + b$$

where  $g_s$  is canopy stomatal conductance estimated from sap flux, the parameter  $b$  is a reference conductance ( $b = g_{s,ref}$ ) at VPD = 1 kPa and the parameter  $-m$  quantifies the sensitivity of  $g_s$  to VPD, and it is equivalent to  $-dg_s/d \ln \text{VPD}$ . A survey of 12 angiosperm tree species and 12 conifer species from the literature showed significant differences in stomatal sensitivity to VPD ( $p < 0.0001$ ). Mean  $-m$  ( $\text{mmol m}^{-2} \text{s}^{-1} \ln(\text{kPa})^{-1}$ ) was 73 and 34 for angiosperms and conifers, respectively, with relatively little overlap between groups (Fig. 4a). The lower sensitivity of conifer stomata to VPD, as compared to angiosperms, may contribute to the large daily losses in conifer leaf hydraulic conductance and the observed wide safety margins between stem and leaf.

Another potential explanation for the differences in safety margins and loss and recovery of hydraulic conductance in angiosperms versus conifers might be differences in their ability to repair embolism. In order to repair embolism, according to current thought on the refilling process [7,8], sugars must be transported into the embolized conduit with water passively following along a gradient in osmotic potential. This sugar and its transport would need to be derived from living cells: either parenchyma or phloem, although an earlier study suggested that transfusion tissue in pine needles may also serve as a source for solutes [52]. Since distance to phloem varies with sapwood depth, one strategy that a plant could employ would be to embed parenchyma throughout the xylem, allowing more conduits access to sugars in the case of embolism.

This strategy may help explain the differences in hydraulic behavior between conifers and angiosperms. In some angiosperms,



**Fig. 4.** Stomatal sensitivity to increases in vapor pressure deficit (VPD) was greater in angiosperms (○) than conifers (▲). (a) Branch nonstructural carbohydrate concentration and parenchyma area (as a percentage of total tangential sapwood area, (b) were also greater in angiosperms than conifers. The parameter  $-m$  is the sensitivity of  $g_s$  to VPD, and it is equivalent to  $-dg_s/d \ln \text{VPD}$ . Stomatal sensitivity data compiled from [44,48–51]. Branch NSC and parenchyma area data compiled from online resources (see text) and [54–56].

live axial and ray parenchyma can account for as much as 40% of the total sapwood volume [53]. In a survey of 14 tree species (seven angiosperms, seven conifers; species selection was based on availability of carbohydrate data and tangential wood section images from main stems (i.e. trunks), parenchyma data were obtained from web sources including The Virtual Plant website at Victoria University, Inside Wood at North Carolina State University and [www.Sciencephoto.com](http://www.Sciencephoto.com); carbohydrate data were from [54–56]), we found that the mean tangential parenchyma area fraction was 25% in angiosperms and only 8% in conifers with no overlap (Fig. 4b). To our knowledge, little is known about the similarity or dissimilarity in ray and axial parenchyma functions in conifers and angiosperms. However, two earlier studies found starch only in axial parenchyma (none in ray parenchyma; [57]) in ten tropical angiosperms, but starch was found in both ray and axial parenchyma in *Pinus strobus* [58]. Furthermore, nonstructural carbohydrate concentration (as a percentage of dry mass) in branch sapwood was 14% in the angiosperms and only 5% in gymnosperms, again with no overlap (Fig. 4b). Interestingly, the ratios of parenchyma area and nonstructural carbohydrate concentrations in angiosperms versus conifers were nearly identical (3.2 and 3.1, respectively, not significantly different). This potential connection

between parenchyma abundance, storage carbohydrates and the ability to refill embolized xylem is consistent with the observation that leaves, with their abundant parenchyma (up to 70% parenchyma volume per leaf volume, [59,60]) and capacity to synthesize sugars also exhibit vigorous embolism reversal [17,27,43]. Although two studies found no difference in axial parenchyma volume in roots versus stems of conifers [61,62], they did observe both larger and more numerous cross-field pits (i.e. pits on the surface of parenchyma that are also in contact with tracheids) in roots versus stems. This would allow for much more pit area to be exposed between root parenchyma and tracheids compared to those in the stem. In general, it appears that roots of angiosperms had more axial parenchyma than stems in both diffuse-porous and ring-porous trees [63, see also 64 and references therein].

As implied above, the potential for generating osmotic gradients to drive refilling of embolized conduits may be achievable due to the presence of nonstructural carbohydrates in nearby tissues. Using an estimate of the average fresh mass to dried mass ratio of wood of 2.3 (DMJ unpublished data, four conifers and four angiosperms, S.E. = 0.1), we can estimate the volume of apoplastic water per wood volume.

$$\frac{\text{volume apoplastic water}}{\text{wood volume}} = \frac{\text{fresh mass} - \text{dry mass}}{(\text{dry mass}/\text{wood density})}$$

This results in an average apoplastic water to wood volume ratio of 0.6, or 0.6 ml of water for every  $\text{cm}^3$  of wood. Using the Van't Hoff relationship [7], 1 mg of starch per gram of fresh weight stem (or 0.6 g of water and 0.4 g of wood) could generate an osmotic gradient of approximately 1 MPa if all of the starch were converted to sucrose. Based on the average NSC concentrations for the angiosperms and conifers from our literature survey, the observed concentrations would result in a maximum osmotic pressure of 2 MPa in conifer wood and 6 MPa in angiosperm wood. Estimates of plant cell membrane hydraulic conductivity vary over several orders of magnitude (e.g.,  $5.1 \times 10^{-6}$ – $2.6 \times 10^{-8} \text{ m s}^{-1} \text{ MPa}^{-1}$ , [65–67]) and can result in required osmotic gradients of 0.2–40 MPa for movement of water from parenchyma into an embolized vessel [7]. Furthermore, reflection coefficients for movement of sucrose from a living parenchyma cell to an embolized conduit have been estimated at 0.5 (where 0 and 1 are all particles and no particles traveling across the membrane, respectively) and membrane permeability coefficients for sucrose have been approximated at  $10^{-6} \text{ m s}^{-1}$  [68]. The magnitude of resistance to solute movement and water flow at the interface between living cells and embolized conduits deserves considerable future research to fully understand the refilling process.

Although multiple studies have shown that phloem activity is necessary for complete hydraulic repair in some species [e.g., 10,31] there could potentially be an interaction between localized nonstructural carbohydrates in parenchyma and compounds transported via the phloem. Some research has suggested [e.g., 69,70] that hormonal signals (e.g., auxins) in the phloem may induce hydrolysis of starch in parenchyma cells near embolized xylem elements. Other research suggested that the energy released by the embolism event was sufficient to induce starch hydrolysis and embolism repair [71]. Conversely, there is evidence that sucrose accumulation on vessel walls results in starch depolymerization in parenchyma cells and refilling of xylem [13]. Although the signals involved in refilling embolized conduits are still unresolved, the majority of evidence points to carbohydrates in nearby parenchyma as the source for the osmotica that drive refilling. We suggest that the same parenchyma may also perform a dual function as a capacitor that transiently discharges water required for refilling.

## 5. Conclusions

Although our understanding of embolism formation and repair is far from complete and even though there is a continuum of hydraulic strategies in both angiosperms and conifers, there are distinctive differences between the two groups that are related to hydraulic function. Conifer stems have greater hydraulic safety margins than those of angiosperms. Distal organs (leaves and roots) of conifers embolize and refill more frequently than those of angiosperms, which could be related to low stomatal sensitivity and/or a lesser ability of conifers to repair stem embolisms. Conifers also have less xylem parenchyma and lower nonstructural carbohydrate concentrations in their stems than angiosperms, both of which may be required for embolism repair. The highly negative safety margins found in conifers are likely a reflection of the relative inefficiency of their stem embolism repair mechanism(s).

Future research should be aimed at understanding the relationship between phloem carbon (i.e. carbon transported through the phloem to sites of embolism) and parenchyma NSC and the signal(s) responsible for hydrolysis of starch in the parenchyma, the fate of carbon used for refilling embolized conduits, and the biophysical properties of the interface between living cells and embolized conduits. One unresolved question is: do conifers have greater safety margins than angiosperms due to (a) less effective repair systems associated with less stem parenchyma and nonstructural carbohydrates; (b) slow stomatal responses; or (c) a relative paucity of carbon compared to angiosperms (less carbon fixed per individual); or some combination of the above?

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## References

- [1] M.H. Zimmermann, Xylem Structure and the Ascent of Sap, Springer Verlag, N.Y., 1983.
- [2] M.T. Tyree, F.W. Ewers, The hydraulic architecture of trees and other woody plants, *New Phytologist* 119 (1991) 345–360.
- [3] N.N. Alder, J.S. Sperry, W.T. Pockman, Root and stem xylem cavitation, stomatal conductance, and leaf turgor in *Acer grandidentatum* across a soil moisture gradient, *Oecologia* 105 (1996) 293–301.
- [4] K.L. Kavanagh, B.J. Bond, S.N. Aitken, B.L. Gartner, S. Knowe, Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings, *Tree Physiology* 19 (1999) 31–37.
- [5] J.-W. Chen, Q. Zhang, X.-S. Li, K.-F. Cao, Independence of stem and leaf hydraulic traits in six Euphorbiaceae tree species with contrasting leaf phenology, *Planta* 230 (2009) 459–468.
- [6] J.-C. Domec, K. Schäfer, R. Oren, H.S. Kim, H.R. McCarthy, Variable conductivity and embolism in roots and branches of four contrasting tree species and their impacts on whole-plant hydraulic performance under future atmospheric CO<sub>2</sub> concentration, *Tree Physiology* 30 (2010) 1001–1015.
- [7] M.A. Zwieniecki, N.M. Holbrook, Confronting Maxwell's demon: biophysics of xylem embolism repair, *Trends in Plant Science* 14 (2009) 530–534.
- [8] A. Nardini, M.A. Lo Gullo, S. Salleo, Refilling embolized xylem conduits: is it a matter of phloem unloading? *Plant Science* 180 (2011) 604–611.
- [9] C.R. Brodersen, A.J. McElrone, B. Choat, M.A. Matthews, K.A. Schackel, The dynamics of embolism repair in xylem: in vivo visualizations using high resolution computed tomography, *Plant Physiology* 154 (2010) 1088–1095.
- [10] S.J. Bucci, F.G. Scholz, G. Goldstein, F.C. Meinzer, L. Da S.L. Sternberg, Dynamic changes in hydraulic conductivity in petioles of two savanna tree species: factors and mechanisms contributing to the refilling of embolized vessels, *Plant, Cell & Environment* 26 (2003) 1633–1645.
- [11] S. Salleo, P. Trifilò, S. Esposito, A. Nardini, M.A. Lo Gullo, Starch-to-sugar conversion in wood parenchyma of field-growing *Laurus nobilis* plants: a component of the signal pathway for embolism repair? *Functional Plant Biology* 36 (2009) 815–825.
- [12] F. Secchi, M.E. Gilbert, M.A. Zwieniecki, Transcriptome response to embolism formation in *Populus trichocarpa* provides insight into signaling and biology of refilling, *Plant Physiology* 157 (2011) 1419–1429.
- [13] F. Secchi, M.A. Zwieniecki, Sensing embolism in xylem vessels: the role of sucrose as a trigger for refilling, *Plant, Cell & Environment* 34 (2011) 514–524.
- [14] V. Zufferey, H. Cochard, T. Ameglio, J.-L. Spring, O. Viret, Diurnal cycles of embolism repair and formation in petioles of grapevine (*Vitis vinifera* cv. Chasselas), *Journal of Experimental Botany* 62 (2011) 3885–3894.
- [15] K. Esau, Anatomy of Seed Plants, 2nd ed., Wiley, New York, 1977.
- [16] J.-C. Domec, B. Lachenbruch, F.C. Meinzer, D.R. Woodruff, J.M. Warren, K.A. McCulloh, Maximum height in a conifer is associated with conflicting requirements for xylem design, *Proceedings of the National Academy of Sciences of the United States of America* 105 (2008) 12069–12074.
- [17] A.R. Ambrose, S.C. Sillett, T.E. Dawson, Effects of tree height on branch hydraulics, leaf structure, and leaf gas exchange in California redwoods, *Plant, Cell & Environment* 32 (2009) 743–757.
- [18] A.J. McElrone, W.T. Pockman, J. Martínez-Vilalta, R.B. Jackson, Variation in xylem structure and function in stems and roots of trees to 20 m depth, *New Phytologist* 163 (2004) 507–517.
- [19] H. Maherali, C.F. Moura, M.C. Caldeira, C.J. Willson, R.B. Jackson, Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees, *Plant, Cell & Environment* 29 (2006) 571–583.
- [20] C.J. Willson, P.S. Manos, R.B. Jackson, Hydraulic traits are influenced by phylogenetic history in the drought-resistant and invasive genus *Juniperus* (Cupressaceae), *American Journal of Botany* 95 (2008) 299–314.
- [21] D.M. Johnson, K.A. McCulloh, F.C. Meinzer, D.R. Woodruff, Hydraulic patterns and safety margins, from stem to stomata, in three eastern US tree species, *Tree Physiology* 31 (2011) 659–668.
- [22] F.C. Meinzer, D.R. Woodruff, J.-C. Domec, G. Goldstein, P.I. Campanello, M.G. Gatti, R. Villalobos-Vega, Coordination of leaf and stem water transport properties in tropical forest trees, *Oecologia* 156 (2008) 31–41.
- [23] M.A. Sobrado, Embolism vulnerability in drought-deciduous and evergreen species of a tropical dry forest, *Acta Oecologica* 18 (1997) 383–391.
- [24] L.S. Santiago, G. Goldstein, F.C. Meinzer, J.B. Fisher, K. Machado, D.R. Woodruff, T. Jones, Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees, *Oecologia* 140 (2004) 543–550.
- [25] K.A. McCulloh, D.M. Johnson, F.C. Meinzer, S.L. Voelker, B. Lachenbruch, J.-C. Domec, Hydraulic architecture of two species differing in wood density: opposing strategies in co-occurring tropical pioneer trees, *Plant, Cell & Environment* 35 (2012) 116–125.
- [26] F.C. Meinzer, D.M. Johnson, B. Lachenbruch, K.A. McCulloh, D.R. Woodruff, Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance, *Functional Ecology* 23 (2009) 922–930.
- [27] F.G. Scholz, S.J. Bucci, G. Goldstein, F.C. Meinzer, A.C. Franco, F. Miralles-Wilhelm, Biophysical properties and functional significance of stem water storage tissues in neotropical savanna trees, *Plant, Cell & Environment* 30 (2007) 236–248.
- [28] U.G. Hacke, J.S. Sperry, W.T. Pockman, S.D. Davis, K.A. McCulloh, Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure, *Oecologia* 126 (2001) 457–461.
- [29] A.L. Jacobsen, F.W. Ewers, R.B. Pratt, W.A. Paddock III, S.D. Davis, Do xylem fibers affect vessel cavitation resistance, *Plant Physiology* 139 (2005) 546–556.
- [30] R.B. Pratt, A.L. Jacobsen, F.W. Ewers, S.D. Davis, Relationships among xylem transport, biomechanics, and storage in stems and roots of nine Rhamnaceae species of the California chaparral, *New Phytologist* 174 (2007) 787–798.
- [31] G. Hao, W.A. Hoffmann, F.G. Scholz, S.J. Bucci, F.C. Meinzer, A.C. Franco, K. Cao, G. Goldstein, Stem and leaf hydraulics of congeneric tree species from adjacent tropical savanna and forest ecosystems, *Oecologia* 155 (2008) 405–415.
- [32] D.M. Johnson, D.R. Woodruff, K.A. McCulloh, F.C. Meinzer, Leaf hydraulic conductance, measured in situ, declines and recovers daily: leaf hydraulics, water potential and stomatal conductance in four temperate and three tropical tree species, *Tree Physiology* 29 (2009) 879–887.
- [33] P. Trifilò, A. Gascò, F. Raimondo, A. Nardini, S. Salleo, Kinetics of recovery of leaf hydraulic conductance and vein functionality from cavitation-induced embolism in sunflower, *Journal of Experimental Botany* 54 (2003) 2323–2330.
- [34] T.J. Brodribb, N.M. Holbrook, Diurnal depression of leaf hydraulic conductance in a tropical tree species, *Plant, Cell & Environment* 27 (2004) 820–827.
- [35] V. Stiller, J.S. Sperry, H.R. Lafitte, Embolized conduits of rice (*Oryza sativa* L., Poaceae) refill despite negative xylem pressure, *American Journal of Botany* 92 (2005) 1970–1974.
- [36] A. Nardini, M. Ramani, E. Gortan, S. Salleo, Vein recovery from embolism occurs under negative pressure in leaves of sunflower (*Helianthus annuus*), *Physiologia Plantarum* 133 (2008) 755–764.
- [37] M.E. McCully, C.X. Huang, L.E.C. Ling, Daily embolism and refilling of xylem vessels in the roots of field-grown maize, *New Phytologist* 138 (1998) 327–342.
- [38] J.-C. Domec, F.G. Scholz, S.J. Bucci, F.C. Meinzer, G. Goldstein, R. Villalobos Vega, Diurnal and seasonal variation in root xylem embolism in neotropical savanna woody species: impact on stomatal control of plant water status, *Plant, Cell & Environment* 29 (2006) 26–35.
- [39] S. Salleo, M.A. Lo Gullo, Drought resistance strategies and vulnerability to cavitation of some Mediterranean sclerophyllous trees, in: M. Borghetti, J. Grace, A. Raschi (Eds.), *Water Transport in Plants under Climatic Stress*, Cambridge University Press, Cambridge, UK, 1993, pp. 99–113.
- [40] U.G. Hacke, J.S. Sperry, Limits of xylem refilling under negative pressure in *Laurus nobilis* and *Acer negundo*, *Plant, Cell & Environment* 26 (2003) 303–311.
- [41] H. Taneda, J.S. Sperry, A case-study of water transport in co-occurring ring-porous trees: contrasts in water-status, conducting capacity, cavitation and vessel refillings, *Tree Physiology* 28 (2008) 1641–1651.

- [43] P.J. Aphalo, P.G. Jarvis, Do stomata respond to relative humidity, *Plant, Cell & Environment* 14 (1991) 127–132.
- [44] R. Oren, J.S. Sperry, G.G. Katul, D.E. Pataki, B.E. Ewers, N. Phillips, K. Schafer, Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit, *Plant, Cell & Environment* 22 (1999) 1515–1526.
- [45] S.E. Bush, D.E. Pataki, K.R. Hultine, A.J. West, J.S. Sperry, J.R. Ehleringer, Wood anatomy constrains stomatal responses to atmospheric vapor pressure deficit in irrigated, urban trees, *Oecologia* 156 (2008) 13–20.
- [46] E.B. Peters, J.P. McFadden, R.A. Montgomery, Biological and environmental controls on tree transpiration in a suburban landscape, *Journal of Geophysical Research: Biogeosciences* 115 (2010), <http://dx.doi.org/10.1029/2009JG001266>.
- [47] E. Litvak, H.R. McCarthy, D.E. Pataki, Transpiration sensitivity of urban trees in a semi-arid climate is constrained by xylem vulnerability to cavitation, *Tree Physiology* 32 (2012) 373–388.
- [48] F.C. Meinzer, J.L. Andrade, G. Goldstein, N.M. Holbrook, J. Cavelier, P. Jackson, Control of transpiration from the upper canopy of a tropical forest: the role of stomatal, boundary layer and hydraulic architecture components, *Plant, Cell & Environment* 20 (1997) 1242–1253.
- [49] B.E. Ewers, S.T. Gower, B. Bond-Lamberty, C.K. Wang, Effects of stand age and tree species on canopy transpiration and average stomatal conductance of boreal forests, *Plant, Cell & Environment* 28 (2005) 660–678.
- [50] B.E. Ewers, D.S. Mackay, S. Samanta, Interannual consistency in canopy stomatal conductance control of leaf water potential across seven tree species, *Tree Physiology* 27 (2007) 11–24.
- [51] B.E. Ewers, D.S. Mackay, J. Tang, P.V. Bolstad, S. Samanta, Intercomparison of sugar maple (*Acer saccharum* Marsh.) stand transpiration responses to environmental conditions from the Western Great Lakes Region of the United States, *Agricultural and Forest Meteorology* 148 (2008) 231–246.
- [52] M.J. Canny, Transfusion tissue of pine needles as a site of retrieval of solutes from the transpiration stream, *New Phytologist* 123 (1993) 227–232.
- [53] A.J. Panshin, C. De Zeeuw, *Textbook of Wood Technology*, McGraw-Hill, New York, NY, 1980.
- [54] G. Hoch, A. Richter, C. Koerner, Non-structural carbon compounds in temperate forest trees, *Plant, Cell & Environment* 26 (2003) 1067–1081.
- [55] A. Sala, G. Hoch, Height-related growth declines in ponderosa pine are not due to carbon limitation, *Plant, Cell & Environment* 32 (2009) 22–30.
- [56] D.R. Woodruff, F.C. Meinzer, Water stress, shoot growth and storage of non-structural carbohydrates along a tree height gradient in a tall conifer, *Plant, Cell & Environment* 34 (2011) 1920–1930.
- [57] S. Fink, Histochemische Untersuchungen über Stärkeverteilung und Phosphataseaktivität Holz einiger tropischer Baumarten, *Holzforschung* 36 (1982) 295–302.
- [58] L. Murmanis, R.F. Evert, Parenchyma cells of secondary phloem in *Pinus strobus*, *Planta* 73 (1967) 301–318.
- [59] B.F. Chabot, J.F. Chabot, Effects of light and temperature on leaf anatomy and photosynthesis in *Fragaria vesca*, *Oecologia* 26 (1977) 363–377.
- [60] S.A. James, W.K. Smith, T.C. Vogelmann, Ontogenetic Differences in mesophyll structure and chlorophyll distribution in *Eucalyptus globulus* ssp. *globulus* (Myrtaceae), *American Journal of Botany* 86 (1999) 198–207.
- [61] P. Denne, S. Turner, Ray structure differences between root-wood and stem-wood in a range of softwood species, *IAWA Journal* 30 (2009) 71–80.
- [62] P. Denne, P. Gasson, Ray structure in root- and stem-wood of *Larix decidua*: implications for root identification and function, *IAWA Journal* 29 (2008) 17–23.
- [63] R.N. Patel, A comparison of the anatomy of the secondary xylem in roots and stems, *Holzforschung* 19 (1965) 72–79.
- [64] C.R. Metcalfe, L. Chalk, *Anatomy of the Dicotyledons*, 2nd ed., Clarendon Press, Oxford, 1979.
- [65] M.A. Zwieniecki, P.J. Melcher, N.M. Holbrook, Hydraulic properties of individual xylem vessels of *Fraxinus Americana*, *Journal of Experimental Botany* 52 (2001) 1–8.
- [66] Y.X. Kim, E. Steudle, Light and turgor affect the water permeability (aquaporins) of parenchyma cells in the midrib of leaves of *Zea mays*, *Journal of Experimental Botany* 58 (2007) 4119–4129.
- [67] C. Maurel, F. Tacnet, J. Guclu, J. Guern, P. Ripoche, Purified vesicles of tobacco cell vacuolar and plasma membranes exhibit dramatically different water permeability and water channel activity, *Proceedings of the National Academy of Sciences of the United States of America* 94 (1997) 7103–7108.
- [68] T. Vesala, T. Hölttä, M.K. Perämäki, E. Nikinmaa, Refilling of a hydraulically isolated embolised vessel: model calculations, *Annals of Botany* 91 (2003) 419–428.
- [69] S. Salleo, M.A. LoGullo, D. DePaoli, M. Zippo, Xylem recovery from cavitation-induced embolism in young plants of *Laurus nobilis*: a possible mechanism, *New Phytologist* 132 (1996) 47–56.
- [70] S. Salleo, P. Trifilò, M.A. Lo Gullo, Phloem as a possible major determinant of rapid cavitation reversal in stems of *Laurus nobilis* (laurel), *Functional Plant Biology* 33 (2006) 1063–1074.
- [71] S. Salleo, P. Trifilò, M.A. Lo Gullo, Vessel wall vibrations: trigger for embolism repair? *Functional Plant Biology* 35 (2008) 289–297.
- [72] F.G. Scholz, N.G. Phillips, S.J. Bucci, F.C. Meinzer, G. Goldstein, Hydraulic capacitance: biophysics and functional significance of internal water sources in relation to tree size, in: F.C. Meinzer, B. Lachenbruch, T.E. Dawson (Eds.), *Size- and Age-Related Changes in Tree Structure and Function*, 2011, pp. 341–361.
- [73] J-C. Domec, S. Palmroth, E. Ward, C.A. Maier, M. Thereuzien, R. Oren, Interactive effects of long term elevated CO<sub>2</sub> and N-fertilization on the coordination between leaf hydraulic conductance and stomatal conductance in *Pinus taeda*, *Plant, Cell & Environment* 32 (2009) 1500–1512.