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Commentary

Xylem recovery from drought-induced embolism: where is the hydraulic point of no return?

Frederick C. Meinzer^{1,3} and Katherine A. McCulloh²

¹USDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331 USA; ²Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331 USA; ³Corresponding author (fmeinzer@fs.fed.us)

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For terrestrial plants, maintenance of the integrity of the root-to-leaf water transport pathway is essential for sustaining photosynthetic gas exchange and growth. The problem of maintaining long-distance water transport is especially challenging in trees because path-length resistances and gravity can result in steep gradients of increasing xylem tension from roots to terminal branches, potentially increasing the risk of tension-induced xylem embolism (Sperry and Tyree 1988). These emboli reduce xylem hydraulic conductance and, under certain conditions, can accumulate rapidly through a process that has been called runaway embolism, which can ultimately lead to catastrophic and irreversible hydraulic failure (Tyree and Sperry 1988). This phenomenon has led to intensive interest in the role of plant hydraulic dysfunction in drought-induced mortality currently taking place in many tree-dominated ecosystems, which is expected to increase under future climate change scenarios (Allen et al. 2010, McDowell et al. 2011, Choat et al. 2012).

The susceptibility of xylem to embolism has traditionally been characterized by generating the so-called xylem vulnerability curves, which are plots of the loss of hydraulic conductivity in relation to xylem tension or pressure (Figure 1, top). Key features of these curves that are often quantified include the embolism threshold (P_e), the xylem pressures corresponding to 50 and 88% loss of conductivity (P_{50} and P_{88}) and the slope of the steep, nearly linear portion of the curve. Thus, highly embolism-resistant xylem might be expected to show a highly negative value of P_e and a gradual slope beyond this point, which would ensure substantially more negative values of P_{50} and P_{88} . However, vulnerability to embolism does not

necessarily equate to risk of embolism in situ, which is partly determined by the influence of stomatal regulation of transpiration on the normal operating range of xylem tension in a given plant organ. Isohydric species tend to show relatively constant maximum values of xylem tension, whereas the maximum xylem tension in anisohydric species varies according to environmental conditions such as soil water availability and vapor pressure deficit (Tardieu and Simonneau 1998, Schultz 2003, Rogiers et al. 2012). However, isohydry and anisohydry represent two extremes of a continuum of regulation of xylem tension.

This limitation on relating the characteristics of xylem vulnerability curves to the actual risk of embolism and hydraulic dysfunction in intact, field-grown plants has contributed to the development of the concept of hydraulic safety margins (Alder et al. 1996, Hacke and Sauter 1996, Pockman and Sperry 2000, Vilagrosa et al. 2003, Brodribb and Holbrook 2004, Meinzer et al. 2009, Hoffmann et al. 2011, Johnson et al. 2012), which can be defined as the difference between the minimum xylem pressure normally attained in a given plant organ and a reference point on its hydraulic vulnerability curve (e.g., P_{50}). Intensive research on plant hydraulic architecture has revealed much about broad patterns of xylem vulnerability to embolism and hydraulic safety margins within plants (e.g., Martinez-Vilalta et al. 2002, Domec and Gartner 2005, Domec et al. 2006a, 2006b, Maherali et al. 2006) and across contrasting vegetation types (Pockman and Sperry 2000, Maherali et al. 2004, Jacobsen et al. 2007, Meinzer et al. 2009, Choat et al. 2012). Nevertheless, simple hydraulic predictors of a species' performance and ability to survive in a specific type of

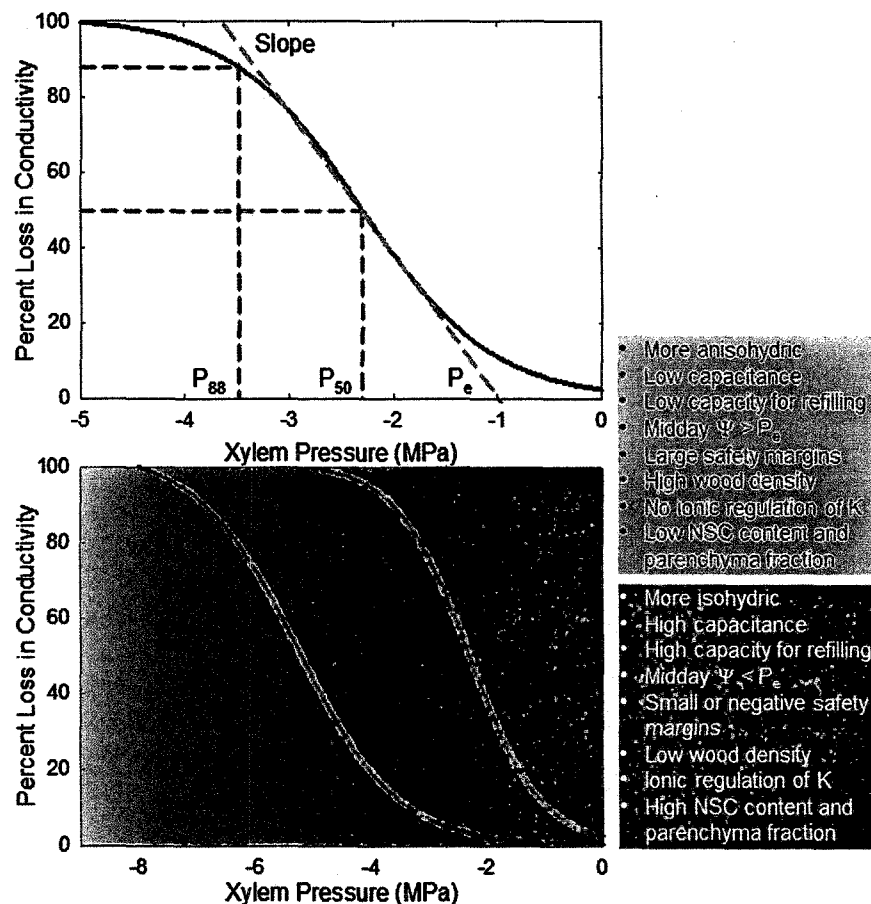


Figure 1. Top: Theoretical xylem vulnerability curve showing key features often used to compare curves. New evidence of the ability of some species to refill embolized conduits means that these parameters may not indicate risk of irreversible failure as much as was previously thought. P_{88} and P_{50} are the pressures at which 88 and 50% of the hydraulic conductivity, respectively, have been lost. The slope of interest is of a line tangential to the curve that runs through the P_{50} . The x-intercept of this line gives the P_e value, which is the pressure of air-entry. Bottom: Two hypothetical stem vulnerability curves from species that differ in their vulnerability to embolism, but not their midday stem water potential (vertical pink line). The text boxes list traits that may be correlated with each species' risk of embolism (see the text for examples). The color transition indicates that the differences depicted represent endpoints along a continuum. Ψ is the water potential, K is the hydraulic conductance and NSC is the non-structural carbohydrate.

drought-prone environment still elude us because there are multiple hydraulic solutions for coping with a given set of environmental constraints.

A critical missing link in our ability to assess the differential risk of catastrophic hydraulic failure among species is knowledge of their ability to recover from embolism-induced loss of hydraulic capacity. Although it is now widely accepted that refilling of embolized xylem conduits in roots, stems and leaves occurs even when nearby functional conduits are still under considerable tension (McCully et al. 1998, Zwieniecki and Holbrook 1998, McCully 1999, Zwieniecki et al. 2000, Holbrook et al. 2001, Melcher et al. 2001, Bucci et al. 2003, Domec et al. 2006a, 2006b, Johnson et al. 2009, Brodersen et al. 2010), there is scanty knowledge of species-specific hydraulic points of no return, that is, levels of embolism beyond which recovery does not occur. In the present issue of *Tree Physiology*, Ogasa et al. (2013) report a substantial variation in the ability of stem xylem to recover from ~50% loss of hydraulic conductivity

among seven angiosperm tree species. Interestingly, and perhaps somewhat surprisingly, the ability of xylem to recover from 50% loss of conductivity was inversely related to species-specific values of P_{50} determined from xylem vulnerability curves. That is, species with the most negative values of P_{50} showed the lowest xylem recovery capacity once their stems had lost about half of their conductivity. These species also showed the largest apparent hydraulic safety margins expressed as the difference between P_{50} and the daily minimum stem water potential. While other studies have reported limits on xylem refilling following tension-induced embolism (Sobrado et al. 1992, Edwards et al. 1994, Tyree et al. 1999; Hacke and Sperry 2003), the study of Ogasa et al. (2013) is among the first to have investigated multiple species in a systematic manner. The generality of the relationships reported by Ogasa et al. (2013) is not known. However, if species with the most embolism-resistant xylem and the largest apparent hydraulic safety margins turn out to be the least resilient in terms of recovery of

hydraulic function once a substantial amount of embolism has occurred, then traditional approaches to characterizing the vulnerability to and risk of catastrophic hydraulic failure may need to be reassessed.

Recent findings suggest that there may be phylogenetic trends in the magnitude of hydraulic safety margins and the capacity of xylem to recover from tension-induced embolism. There appears to be a tendency for conifer stems to have larger hydraulic safety margins when compared with most angiosperm stems (Meinzer et al. 2009, Choat et al. 2012, Johnson et al. 2012), with Mediterranean climate angiosperms being a potential exception. Conifers are reputed to have a lower capacity to recover from drought-induced embolism when compared with angiosperms (e.g., Brodribb et al. 2010), but this has not been studied systematically in either group and only limited evidence suggests that some conifers may indeed be able to regularly refill embolized tracheids (Zwieniecki and Holbrook 1998). A detailed discussion of potential mechanisms involved in refilling of embolized xylem conduits is beyond the scope of this Commentary, but a role for sugars released from the starch stored in xylem parenchyma has been implicated (Salleo et al. 2009, Nardini et al. 2011a, Secchi and Zwieniecki 2012). If this were the case, then the tendency for lower xylem parenchyma volume fractions in conifer than in angiosperm stems should be associated with more conservative (larger) hydraulic safety margins and a lower xylem refilling capacity in conifers than in angiosperms at comparable levels of embolism (Johnson et al. 2012).

As indicated above, stomatal control of transpiration-induced xylem tension is an obvious mechanism for avoiding excessive embolism. Additional features contributing to the avoidance of hydraulic points of no return under dynamic conditions include capacitive discharge of water into the transpiration stream to buffer fluctuations in xylem tension (Meinzer et al. 2003, Scholz et al. 2007, Hölttä et al. 2009) and rapid increases in the ionic concentration of xylem sap that increase the conductivity of functional conduits (Nardini et al. 2011b, 2012). The intrinsic capacitance of stem sapwood is positively correlated with daily minimum stem water potentials and is inversely correlated with xylem resistance toward embolism, making capacitance a key component of hydraulic safety margins (Meinzer et al. 2008, 2009). Diurnal increases in the ionic concentration of xylem sap can partly compensate for the embolism-induced loss of conductivity, thereby constraining further increases in xylem tension that could increase the risk of runaway embolism (Trifilò et al. 2008, 2011).

Ogasa et al. (2013) have shown that there is a continuum with regard to how readily plants can recover from drought-induced declines in hydraulic conductivity and that xylem recovery capacity is correlated with other traits such as resistance towards embolism. Yet, the specific traits governing xylem recovery capacity remain unclear (Figure 1, bottom). The two vulnerability curves shown in Figure 1 (bottom) repre-

sent hypothetical species at the endpoints of this continuum of xylem recovery capacity and the vertical pink line indicates their midday stem water potential. At this midday water potential, the species on the right is predicted to lose the majority of its hydraulic conductivity, while the species on the left will not. Many traits tend to correlate with each of the contrasting vulnerability curves, but it is not clear which trait leads to the ability to refill after embolism formation. For example, while a mechanistic link between non-structural carbohydrate content and xylem parenchyma fraction is easily envisioned for an energy-requiring process such as refilling, it is uncertain how this continuum may relate to traits such as degree of isohydry and ionic regulation of xylem conductance. In conclusion, the hydraulic resilience of a species is determined by multiple physiological and structural traits. Understanding how these traits are integrated at the organismal level to yield adequate hydraulic fitness in a given environment would be a fertile area for future research. This type of information is essential for realistic predictions of species hydraulic limits under current and future climate change scenarios.

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