CONCEPTS, REVIEWS AND SYNTHESES

The blind men and the elephant: the impact of context and scale in evaluating conflicts between plant hydraulic safety and efficiency

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Abstract Given the fundamental importance of xylem safety and efficiency for plant survival and fitness, it is not surprising that these are among the most commonly studied features of hydraulic architecture. However, much remains to be learned about the nature and universality of conflicts between hydraulic safety and efficiency. Although selection for suites of hydraulic traits that confer adequate plant fitness under given conditions is likely to occur at the organismal level, most studies of hydraulic architecture have been confined to scales smaller than the whole plant, such as small-diameter branches and roots. Here we discuss the impact of the spatial and temporal contexts in which hydraulic traits are studied on the interpretation of their role in maintaining plant hydraulic function. We argue that further advances in understanding the ecological implications of different suites of plant hydraulic traits will be enhanced by adopting an integrated approach that considers variation in hydraulic traits throughout the entire plant, dynamic behavior of water transport, xylem tension and water transport efficiency in intact plants, alternate mechanisms that modulate hydraulic safety and efficiency, and alternate measures of hydraulic safety and safety margins.

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Introduction

Land plants transport massive amounts of water from roots to leaves to sustain the transpiration associated with photosynthetic carbon dioxide (CO_2) uptake. Resistance to transpiration-induced flow of water through the xylem creates a gradient of increasing tension between the roots and the most distal leaves. Transport of water under tension makes the xylem susceptible to the formation of air-seeded emboli that break the cohesion of the water column, disabling parts or eventually all of the water conducting system. Xylem structural features that increase its resistance to embolism typically decrease its hydraulic conductivity, leading to potentially conflicting requirements for safety and efficiency of long-distance water transport. Although efficiency can be defined in a number of ways in physics, engineering, and economics, here we mean either the volume flow rate of water per pressure gradient (conductivity) or the flow rate in relation to the overall root-to-leaf driving force at the whole-plant level (conductance). The potential safety/efficiency dilemma is particularly acute for tall trees in which gravity and considerable path-length resistances act in concert to increase the tension gradients necessary to drive water transport to their uppermost branches (Koch et al. 2004; Woodruff et al. 2004; Ryan et al. 2006; Domec et al. 2008). We propose that to better understand the nature of trade-offs of safety against efficiency and when and where they occur, the questions being addressed need to be precisely defined, taking into account the scale at which measurements are made and the temporal context in

which plants are studied. Otherwise, we risk the predicament faced by the proverbial six blind men and the elephant, who arrive at seemingly incompatible conclusions concerning its nature after each has examined only a small portion of it.

Studies of plant hydraulic architecture have provided important insights into the multiple ways that evolution has resolved competing requirements for the safety and efficiency of water transport and mechanical support of the plant body by xylem and other tissues to achieve adequate distribution of water throughout complex vascular networks (West et al. 1999; McCulloh et al. 2003, 2004, 2010; Sperry et al. 2008). Hydraulic architecture has been characterized at scales ranging from the structural features of individual xylem conduits (e.g. Sperry and Hacke 2004; Pittermann et al. 2005, 2006; Wheeler et al. 2005; Domec et al. 2006; Rosner et al. 2007; Hacke and Jansen 2009) to the hydraulic properties of organs, such as stems and roots (e.g., Martinez-Vilalta et al. 2002; Maherali et al. 2006; Willson et al. 2008), to plant-level patterns of hydraulic architecture, such as maps of hydraulic characteristics and ratios of leaf area to conducting xylem area (e.g. Huber 1928; Zimmermann 1978; McDowell et al. 2002; Ackerly 2004; Wright et al. 2006; Dunham et al. 2007; Meinzer et al. 2008a). These studies have contributed to a broad-scale understanding of trends in hydraulic architecture along environmental gradients, strategies of different plant functional groups for coping with water stress, and community level differences in hydraulic architecture (Pockman and Sperry 2000; Maherali et al. 2004; Jacobsen et al. 2007, 2008; Pratt et al. 2007). An issue in interpretation, however, is that most studies of hydraulic architecture have been confined to scales smaller than the whole plant, such as small-diameter branches or roots, whereas selection for suites of hydraulic traits that confer adequate plant fitness under given conditions is likely to occur at the organismal level. Even in environments characterized by extreme drought, commonly measured branch-level hydraulic traits often exhibit wide variation rather than convergence among co-occurring species (e.g., Pockman and Sperry 2000; Maherali et al. 2004; Jacobsen et al. 2007, 2008), implying that complex suites of higher order hydraulic traits contribute to overall fitness and reproductive success in a given environment.

Given the fundamental importance of xylem safety and efficiency for plant survival and fitness, it is not surprising that these are among the most commonly studied features of hydraulic architecture. Typically xylem safety is expressed in terms of the xylem pressure causing 50% loss of hydraulic conductivity (P_{50}), and xylem efficiency is expressed as specific conductivity (k_s), the hydraulic conductivity per unit conducting xylem area. The extent to which xylem safety and efficiency are antagonistic features

leading to inevitable trade-offs has been debated (Maherali et al. 2004, 2006; Willson et al. 2008). In woody plants, these attributes are most frequently characterized in terminal branches and less often in other parts of the plant, such as roots (Martinez-Vilalta et al. 2002; Domec et al. 2004, 2006; Maherali et al. 2006; Pratt et al. 2007; Willson et al. 2008), main stems (Spicer and Gartner 2001; Domec and Gartner 2003; Domec et al. 2005, 2006; Beikircher and Mayr 2008), and leaves (Sack et al. 2003; Brodribb and Holbrook 2004a; Woodruff et al. 2008; Johnson et al. 2009a, b). Although plant organs can be characterized in terms of their own hydraulic architecture, recognition of the spatial and temporal contexts in which they are being studied is essential for interpretation of their role in plant hydraulic function. This is the subject of the remainder of this paper.

What are the variables that can confound interpretation of relationships between xylem safety and efficiency?

We often debate the presence or absence of trade-offs between hydraulic safety and efficiency. However, the hydraulic safety and efficiency of a particular plant part (such as a small-diameter branch) are not necessarily species-specific traits: they may differ greatly from part to part of the plant, and the within-plant pattern itself may vary greatly between taxa with divergent evolutionary histories. Moreover, the contribution of a plant segment to the plant's overall hydraulic architecture is influenced strongly by factors beyond the segment itself. Important confounding factors include the diameter of the segment and its relative axial position along the continuum from roots to leaves as these affect the magnitude of xylem conductivity and tensions developed as well as the timing of maximum water flux, which is often attained substantially later in main stems than in terminal branches because of internal capacitance (Phillips et al. 1997; Goldstein et al. 1998). Also important are the relative quantities and transport characteristics of leaf area, sapwood area, and root-absorbing area (Whitehead et al. 1996; Pataki et al. 1998; Sperry et al. 1998). Another set of factors relates to time-dependent physiology at daily, seasonal, and annual scales, such as the accessibility and properties of water storage tissues, daily and seasonal changes in transpiration with respect to climate and phenology, changes in k_s with variable factors, such as the rate of water transport (Domec et al. 2007), occurrence, and reversal of xylem embolism (Zwieniecki and Holbrook 1998; Bucci et al. 2003), changes in membrane permeability (McElrone et al. 2007), and seasonal changes in leaf (Bucci et al. 2005) or fine root area. It is not possible to infer the integrated impact of

these contextual variables from measurements of k_s and P_{50} on xylem segments or from retrospective estimates of k_s and P_{50} based on anatomy and density of preserved xylem samples. Leaves, the terminal portion of the liquid water transport pathway, undergo rapidly reversible changes in their hydraulic conductance and therefore appear to play a particularly important role in the dynamic regulation of plant hydraulic architecture (e.g., Zwieniecki et al. 2000; Bucci et al. 2003; Brodribb and Holbrook 2004b; Woodruff et al. 2007; Johnson et al. 2009b).

Here we present a series of examples illustrating some of the consequences of scale and context for interpretations of hydraulic architecture and how intact plants resolve potentially conflicting requirements for safety and efficiency of water transport. We argue that integrating information obtained at different scales into an organismal assessment of hydraulic architecture is likely to be the most effective and informative approach for understanding the ecological implications of different suites of plant hydraulic traits.

Use of small-diameter branch samples

When measurements are restricted to segments of terminal branches, interpretations of relationships between P_{50} and k_s across species and environments can be confounded by unrecognized variables and their interactions that lead to apparent decoupling of the safety/efficiency trade-off frequently observed at various scales within species. Xylem conduit diameter typically increases with stem diameter, both within and among species (Fig. 1a), especially over the range of stem diameter most frequently used for studies of comparative hydraulic architecture (approx. 2–15 mm). Because hydraulic conductivity increases as a function of the conduit radius to the fourth power, relatively small variation in stem segment and conduit diameter can be expected to have a disproportionate impact on the values of hydraulic conductivity measured. In practice, hydraulic conductivity and k_s have been observed to increase by about an order of magnitude with a doubling of stem diameter for stem diameters ranging from about 1 to 20 mm (Fig. 1b; Tyree et al. 1991; Zotz et al. 1998; Cochard et al. 1999; McCulloh et al. 2010). Given that the dependence of P_{50} on conduit diameter is relatively weak (Tyree et al. 1994; Hacke et al. 2001; Willson et al. 2008), comparisons of hydraulic efficiency and safety based on measurements of terminal branch segments can be expected to yield large variation in k_s relative to P_{50}, which is likely to lead to the conclusion that a trade-off of xylem efficiency against safety is apparently absent. Even when the conductivity-weighted mean conduit diameter ($[\sum d^4/n]^{1/4}$, McCulloh et al. 2010) of segments is similar among species having the same conduit and wood type,

their k_s can differ dramatically (Fig. 2) further complicating interpretations of relationships between hydraulic efficiency and safety. In the example shown in Fig. 2, the mean number of vessels per cross-sectional area of the temperate diffuse-porous species was several fold higher than that of the tropical diffuse-porous species, resulting in substantially greater k_s in the temperate species at a given mean vessel hydraulic diameter (McCulloh et al. 2010). The trajectories of relationships between k_s and P_{50} may be distinct for these two groups of species as has been observed in comparisons of k_s and P_{50} in stem segments from other groups of species (Piñol and Sala 2000). Thus, the apparent presence or absence of an inverse relationship between k_s and P_{50} based on measurements made on stem segments may be somewhat fortuitous depending on the species sampled and the relative positions of the segments along the root-to-terminal branch hydraulic continuum in each species.

Another example is the statistical work of Dunham et al. (2007, 2008) in which relationships among anatomical, hydraulic, and density traits were sought for seven positions within 32 *Pseudotsuga menziesii* trees. The k_s of branch samples with a cambial age of 7 years was not
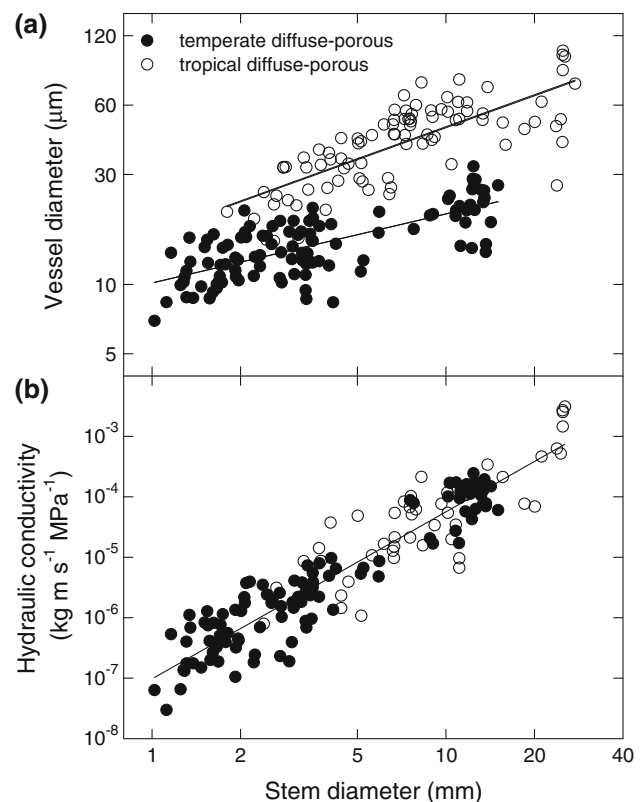
Fig. 1 Relationships between hydraulic traits and stem diameter for saplings of four temperate and four tropical diffuse-porous tree species: **a** vessel diameter, **b** hydraulic conductivity. Each *data point* represents an individual branch or trunk segment. Data taken from McCulloh et al. (2010)
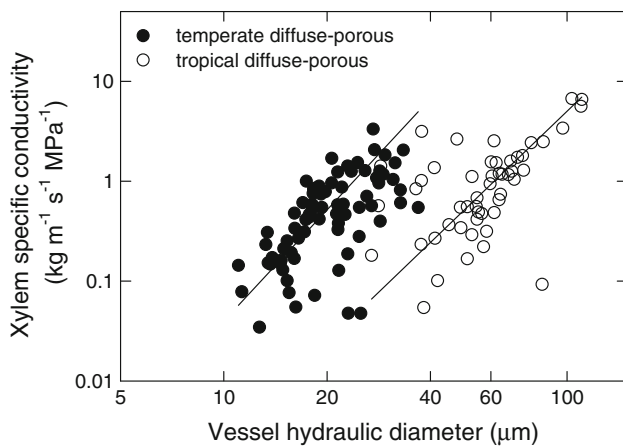
Fig. 2 Relationships between xylem-specific conductivity and mean vessel hydraulic diameter in branch and trunk segments of saplings of four temperate and four tropical diffuse-porous tree species. Data from McCulloh et al. (2010)

correlated with the k_s of branch samples of other ages, stem samples of three ages, or root samples of two ages (Dunham et al. 2007). Moreover, the relationship between tracheid diameter and k_s of branches was extremely different from that relationship for any of the other plant parts studied (Dunham et al. 2008). Seven-year-old branch samples, similar to the samples used in many studies, were a very poor predictor of characteristics elsewhere in the tree. The generalizations one can make with the population of 7-year-old samples is valid, but they should not be extrapolated beyond the dataset without further knowledge. This constraint can be particularly acute in conifers, which often undergo pronounced ontogenetic changes in the hydraulic characteristics of their wood (Mencuccini et al. 1997; Spicer and Gartner 2001; Domec and Gartner 2002a; Rosner et al. 2006).

Because the transport of water from roots to transpiring leaves involves a complex xylem network, the hydraulic properties of a given plant segment represent a snapshot of a unique solution to competing demands for efficiency and safety of water transport that are integrated with the properties of the pathway both upstream and downstream from the segment as well as overall plant architecture and physiology. Based on these considerations, we suggest that comparative studies of the role of safety and efficiency in hydraulic architecture should routinely take into account a greater fraction of the root-to-leaf hydraulic continuum in order to capture patterns of efficiency and safety along the plant axis (see below).

Water storage and the dynamics of water transport

Recent work suggests that other dimensions of safety and efficiency beyond xylem vulnerability and hydraulic

conductivity need to be considered, especially under the dynamic conditions that prevail when plants are transpiring (Meinzer et al. 2008b, 2009; Hölttä et al. 2009). Hydraulic capacitance (C) results in the transient release of stored water into the transpiration stream when the onset of transpiration generates a water potential disequilibrium within the xylem and between the xylem and surrounding tissues. The dual consequences of this phenomenon are that the rate of fluctuation in xylem tension is slowed, damping the amplitude of diel fluctuations in xylem tension (Cowan 1972; Phillips et al. 1997; Perämäki et al. 2005; Scholz et al. 2007, 2008; Hölttä et al. 2009), and the total soil-to-leaf hydraulic conductance transiently appears to be greater than it would under steady-state conditions (Andrade et al. 1998; Meinzer et al. 1999). Capacitive discharge of water can result from emptying of xylem elements, which can still buffer fluctuations in xylem tension despite the marginal loss of conductivity (Hölttä et al. 2009). However, in the sapwood of species such as tropical angiosperms where the volume of water in vessel lumens is small relative to that in other cells and tissues, embolism is a minor source of capacitance over the normal physiological operating range of sapwood water potential (Meinzer et al. 2008b). Contributions of capacitance to hydraulic safety and apparent hydraulic efficiency are most readily observed in intact plants subjected to dynamic conditions and cannot easily be inferred from steady state measurements of hydraulic properties of segments of plant organs under laboratory conditions.

These points can be illustrated by hydraulic functional traits of several Panamanian tree species (Fig. 3). A plot of k_s versus P_{50} of terminal branch segments suggests the absence of a safety versus efficiency trade-off (Fig. 3a), yet there are highly significant positive relationships between P_{50} and sapwood capacitance (Fig. 3b) and daily minimum terminal branch water potential (Fig. 3c). Thus, under the transient conditions that prevail throughout most of the day, the buffering effect of C on minimum xylem Ψ confers a measure of hydraulic safety in species with the highest C and least negative values of P_{50}. Conversely, species with low C appear to rely on xylem structural features that lower P_{50} rather than buffer fluctuations in stem water potential (Meinzer et al. 2009). The contribution of C to hydraulic safety and the inverse relationship between C and wood density (Pratt et al. 2007; Scholz et al. 2007; Meinzer et al. 2008a) could confound the expected positive correlation between wood density and hydraulic safety (Hacke et al. 2001). Wood density of the species included in Fig. 3 ranged from 0.33 to 0.74 g cm^{-3}, but it was not significantly correlated with P_{50} (Meinzer et al. 2008b). The lack of a consistent relationship between P_{50} and wood density has been reported in other studies (e.g., Jacobsen et al. 2008).
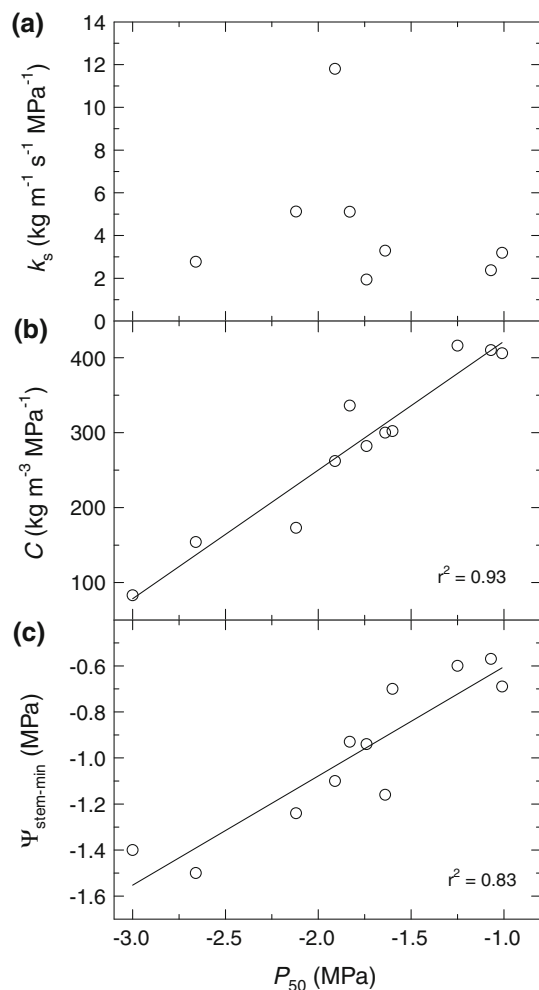
Fig. 3 Relationships between the xylem pressure causing a 50% loss of hydraulic conductivity (P_{50}) and maximum specific conductivity (k_s) (**a**), sapwood capacitance (C) (**b**), and daily minimum water potential ($\Psi_{stem-min}$) (**c**) for upper canopy branches of several Panamanian tree species. Each *point* represents a different species. Data from Meinzer et al. (2008a, b)

Plant architectural adjustments

The ability to regulate whole-plant leaf-specific conductance in response to changing water availability and evaporative demand can influence both hydraulic efficiency and safety in the absence of changes in k_s and P_{50}. *Pinus palustris* trees growing in a xeric site had lower leaf area to sapwood area ratios (A_L:A_S) and were shorter in stature than trees growing in a mesic site, resulting in similar leaf-specific conductance and soil-to-leaf water potential differences among sites (Addington et al. 2006). Similarly, A_L:A_S of ponderosa pine trees growing in a desert environment was about half that of trees growing in a humid montane environment contributing to substantially greater whole-tree leaf-specific conductance in the desert-grown trees and similar values of midday shoot water

potential in both sites (Maherali and DeLucia 2001). In Brazilian savanna trees, mean whole-plant leaf-specific conductance was higher during the dry season than during the wet season as a result of seasonal reductions in A_L:A_S, which allowed midday shoot water potentials to remain nearly constant seasonally (Bucci et al. 2005). Species-specific differences in the plasticity of tree architecture (A_L:A_S) and, therefore, the stability of leaf-specific conductance and maximum xylem tensions could complicate interpretation of the relationships between k_s and P_{50} among species and across environmental gradients.

The preceding observations suggest that xylem safety and efficiency relationships may differ in isohydric and anisohydric species. Isohydric species, which appear to rely on architectural adjustments and capacitance as well as stomatal control to constrain fluctuations in xylem tension, may have less negative values of P_{50} for a given value of k_s than anisohydric species. The limited available evidence is consistent with isohydric species being both more vulnerable to embolism and having a greater capacity for embolism reversal than anisohydric species (e.g., Vogt 2001; Taneda and Sperry 2008). Anisohydric species, in turn, may be more likely to rely on conduit structural attributes (P_{50}) to ensure an adequate degree of hydraulic safety if the embolism experienced in their woody tissues is essentially irreversible. Thus, for a given value of k_s, anisohydric species may have substantially more negative values of P_{50} than isohydric species (Vogt 2001; Oliveras et al. 2003; Maherali et al. 2006; Willson et al. 2008), potentially confounding interpretations of safety versus efficiency trade-offs among species. More information is needed on species-specific patterns of embolism reversal in secondary xylem of iso- and anisohydric species.

How prevalent is the xylem safety versus efficiency trade-off?

The degree to which xylem safety versus efficiency trade-offs are universal is difficult to ascertain because of the ambiguities associated with the interpretation of values of k_s and P_{50} and the observation that P_{50} of stem xylem appears to be avoided under all but the most extreme conditions (Sperry et al. 1993; Sparks and Black 1999; Nardini and Salleo 2000). In many species, stomatal control of transpiration limits maximum xylem tension in stems to a value near the air entry or embolism threshold corresponding to about a 12% loss of conductivity (P_{12}) on the xylem vulnerability curve under typical non-extreme conditions (Sparks and Black 1999; Brodribb et al. 2003; Meinzer et al. 2009). Within the relatively few species for which adequate data are available, the presence of the safety versus efficiency trade-off is remarkably consistent
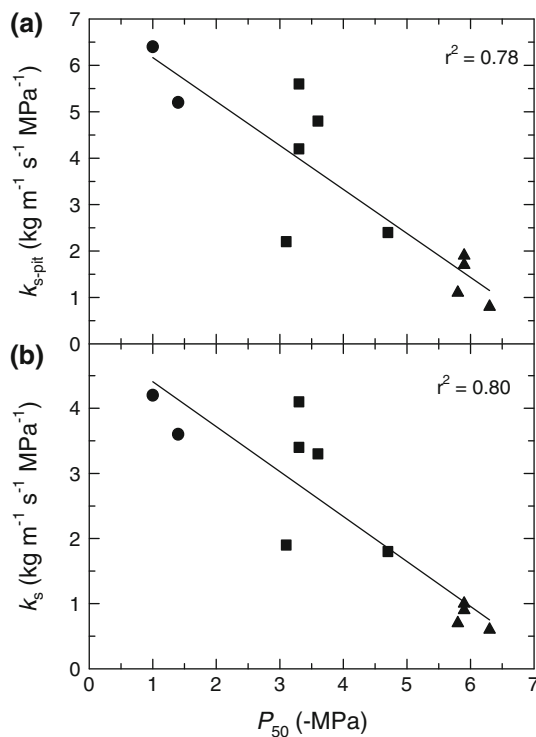
Fig. 4 Relationships between the xylem pressure causing 50% loss of hydraulic conductivity (P_{50}) and maximum bordered pit conductivity on a tissue basis ($k_{s\text{-pit}}$) (**a**) and on whole-wood maximum specific conductivity (k_s) (**b**) for roots (*circle*), trunks (*square*) and branches (*triangle*) of *Pseudotsuga menziesii* trees. Data taken from Domec et al. (2006)

over a broad range of scales from conduits to whole wood and along an axial gradient from roots to branch tips and leaves (Fig. 4; Sperry and Saliendra 1994; Domec and Gartner 2003; Domec et al. 2006; Rosner et al. 2007). Nevertheless, in some species, xylem safety and efficiency appear to be loosely coupled or even positively correlated rather than showing a trade-off under certain conditions. Within growth rings of *Pseudotsuga menziesii*, the k_s of latewood was about an order of magnitude lower than that of earlywood, yet latewood was initially more vulnerable to embolism at xylem pressures down to about −2 MPa (Domec and Gartner 2002b). In *Sequoia sempervirens*, P_{50} decreased substantially with increasing height, yet k_s remained essentially constant or increased slightly (Burgess et al. 2006; Ambrose et al. 2009). Branch sapwood of five Brazilian savanna tree species subjected to 5 years of nitrogen fertilization was significantly more resistant to embolism, yet it was more conductive than sapwood of unfertilized control trees (Bucci et al. 2006). In some cases, variation in wood density has been used as a proxy for trends in P_{50} and k_s, with P_{50} becoming more negative and k_s decreasing with increasing wood density (e.g., Hacke et al. 2001; Bucci et al. 2004; Meinzer et al. 2008a). However, in some of the preceding examples and others

(e.g., Dunham et al. 2007; Jacobsen et al. 2008), no consistent relationships between wood density and hydraulic traits were found, and even inverse relationships between embolism resistance and wood density have been observed (Domec and Gartner 2002a; Bucci et al. 2006).

Understanding the mechanisms responsible for the variation in relationships between xylem safety and efficiency requires comprehensive analyses over a broad range of scales from conduit structure to whole-plant hydraulic architecture. There have been multiple evolutionary solutions to the physiological problem of sustaining water transport to leaves while ensuring an adequate degree of hydraulic safety, and natural selection has resulted in these issues being resolved at the organismal level. Therefore, multi-species comparisons of relationships between hydraulic safety and efficiency must be carefully designed and the questions being addressed precisely defined. Although the prevailing pattern is likely to consist of a trade-off of k_s against P_{50} along the hydraulic continuum from roots to terminal branches in most species, comparisons based on properties of branch segments alone may not be the most reliable indicators of the prevalence of this pattern. Multi-species comparisons incorporating branch segment data sometimes show a weak or no relationship between k_s and P_{50}, yet mean community level P_{50} typically changes in the expected direction along gradients of increasing aridity (Kavanagh et al. 1999; Pockman and Sperry 2000; Maherali et al. 2004). Substantial intracommunity variation in P_{50} among different plant functional types and growth forms (Pockman and Sperry 2000; Maherali et al. 2004; Jacobsen et al. 2007) is consistent with each species having found a somewhat independent evolutionary solution to competing demands for safety and efficiency of water transport, making it difficult to detect the degree of coupling between xylem safety and efficiency across species based on properties of a small fraction of the plant hydraulic pathway.

What do axial trends in xylem safety and efficiency within individuals reveal?

Trajectories of relationships between k_s and P_{50} or P_{12} along the plant hydraulic continuum from roots to branch tips can provide important insights into how species with different wood types and growth forms reconcile competing requirements for efficiency and safety of water transport. Although a number of studies contain data on k_s and P_{50} in roots and terminal branches (e.g., Martinez-Vilalta et al. 2002; Oliveras et al. 2003; Maherali et al. 2006; Pratt et al. 2007), few studies contain detailed data on axial trends in k_s and P_{50} or P_{12} for intermediate points along the hydraulic pathway. When sufficient data are available,

regressions fitted to axial trends in k_s and P_{50} can be extrapolated to the value of P_{50} at which k_s would fall to zero (e.g., Fig. 5a). This point can represent an absolute upper limit of hydraulic safety for a species at which water transport approaches zero regardless of the driving force. In the tall conifer *Pseudotsuga menziesii*, the predicted tree height at which tracheid pit aperture conductance approached zero was consistent with historic maximum height records for the species (Domec et al. 2008). The extrapolated value of P_{50} at which k_s would approach zero in *Pinus ponderosa* (Fig. 5a) is consistent with its shorter maximum height (approx. 60 m) than *P. menziesii* (approx. 120 m). It is not known whether similar relationships exist in other tall coniferous or angiosperm species, but it is likely that their trajectories vary among growth forms having different degrees of branching and apical dominance. The slopes of relationships between k_s and P_{50} or P_{12} can provide insights on differences among species in the steepness of axial tension gradients as well as the loss of hydraulic efficiency associated with a given increment in hydraulic safety.

Measurements only on roots and stems can also be used to generate trajectories of relationships between k_s and P_{50} (Fig. 5b). However, the interpretation of these trajectories is somewhat uncertain because of variable path lengths between sampling locations among individuals of different species and differences in axial trends in hydraulic efficiency among species with different wood types (McCulloh et al. 2010). Nevertheless, data from several studies suggest consistently lower values of k_s and more negative values of P_{50} in stems than in roots and substantial differences among species groups in values of P_{50} for a given range of k_s (Fig. 5b). The pattern seen in several ring-porous (*Quercus*) species is particularly intriguing in that although k_s was sharply reduced in branches compared to roots, P_{50} was only slightly more negative in branches than in roots. This seemingly maladaptive pattern may be associated with hydraulic architectural traits specific to *Quercus* and other ring-porous genera. These include the substantial loss of branch xylem conductivity on a daily basis and vigorous refilling of vessels overnight (Zwieniecki and Holbrook 1998; Taneda and Sperry 2008) and a reduction in sap velocity with decreasing stem diameter in contrast to the more commonly observed increase in velocity in diffuse-porous species and conifers (Huber and Schmidt 1936; Andrade et al. 1998). Declining sap velocity from trunks to terminal branches would partially offset the effect of reduced k_s on xylem tension gradients. Inspection of individual data points for root and stem k_s and P_{50} for 14 diffuse-porous species reveals appreciable overlap between root and stem data, but the overall pattern is consistent with a trade-off (Fig. 5c). Evidence for a trade-off is less convincing based on stem data alone. Principal drivers of the
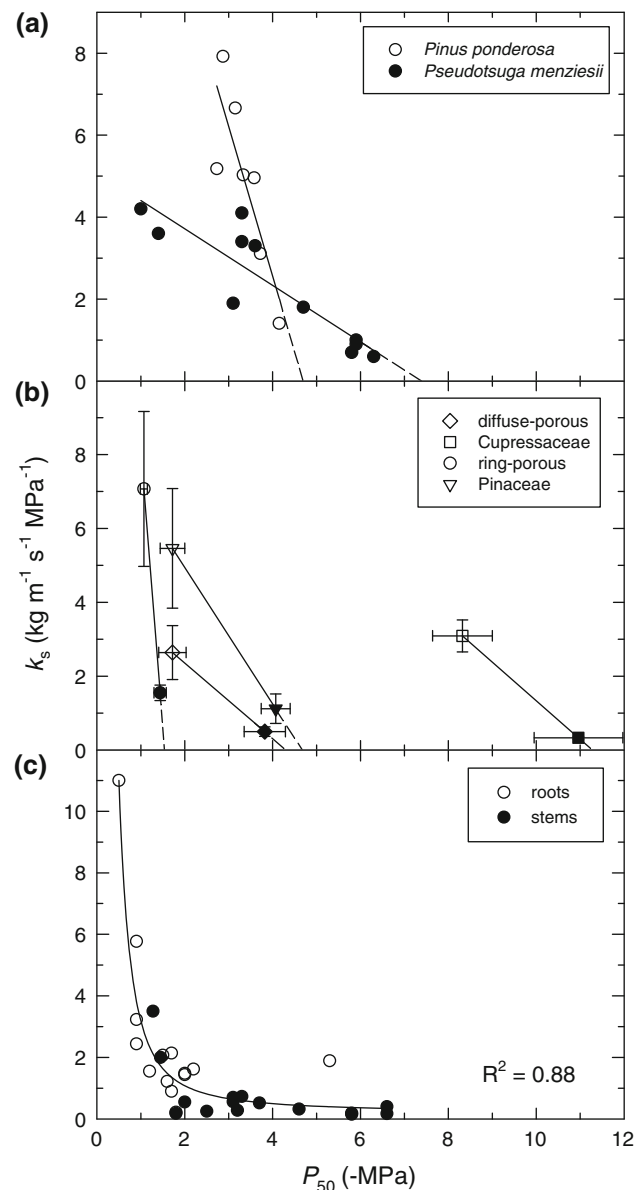
Fig. 5 Relationships between maximum xylem-specific conductivity (k_s) and the xylem pressure causing a 50% loss of hydraulic conductivity (P_{50}) for: **a** different points along the root-to-branch pathway in *Pinus ponderosa* and *Pseudotsuga menziesii* trees (data from Domec and Gartner 2003; Domec et al. 2006), **b** roots (*open symbols*) and branches (*filled symbols*) of 14 temperate diffuse-porous species (data from Sperry and Saliendra 1994; Martinez-Vilalta et al. 2002; Maherali et al. 2006), 14 species of Cupressaceae (data from Maherali et al. 2006; Willson et al. 2008), six Quercus (ring-porous) species (data from Martinez-Vilalta et al. 2002; Maherali et al. 2006) and nine species of Pinaceae (data from Oliveras et al. 2003; Maherali et al. 2006; Hacke and Jansen 2009), **c** 14 temperate diffuse-porous species (data from Sperry and Saliendra 1994; Martinez-Vilalta et al. 2002; Maherali et al. 2006). *Vertical* and *horizontal bars* in **b** represent standard errors, and *each point* in **c** represents a root or stem of a different species

axial safety versus efficiency trade-offs depicted in Fig. 5 include the gradient of increasing tension associated with cumulative path-length resistance from roots to branch tips

and axial trends in conduit taper and leaf-specific conductivity that maximize overall plant transport efficiency per growth investment within mechanical stability constraints (McCulloh and Sperry 2005; Sperry et al. 2008).

Conclusions

A growing body of work over the past two decades has rapidly advanced our understanding of plant hydraulic architecture from minute structural features of xylem conduits to scaling of properties in entire xylem networks. Further advances in understanding the ecological implications of different suites of plant hydraulic traits will be enhanced by adopting an integrated approach that considers variation in hydraulic traits throughout the entire plant, dynamic behavior of water transport, xylem tension and water transport efficiency in intact plants, alternate mechanisms that modulate hydraulic safety and efficiency, and alternate measures of hydraulic safety and safety margins. This approach implies formidable logistical challenges but should serve to minimize the dilemma faced by the six blind men and the elephant whose perceptions about the nature of the beast depended on the part of it being studied.

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