

Safety and efficiency conflicts in hydraulic architecture: scaling from tissues to trees

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ABSTRACT

Tree hydraulic architecture exhibits patterns that propagate from tissue to tree scales. A challenge is to make sense of these patterns in terms of trade-offs and adaptations. The universal trend for conduits per area to decrease with increasing conduit diameter below the theoretical packing limit may reflect the compromise between maximizing the area for conduction versus mechanical support and storage. Variation in conduit diameter may have two complementary influences: one being compromises between efficiency and safety and the other being that conduit tapering within a tree maximizes conductance per growth investment. Area-preserving branching may be a mechanical constraint, preventing otherwise more efficient top-heavy trees. In combination, these trends beget another: trees have more, narrower conduits moving from trunks to terminal branches. This pattern: (1) increases the efficiency of tree water conduction; (2) minimizes (but does not eliminate) any hydraulic limitation on the productivity or tissue growth with tree height; and (3) is consistent with the scaling of tree conductance and sap flow with size. We find no hydraulic reason why tree height should scale with a basal diameter to the two-thirds power as recently claimed; it is probably another mechanical constraint as originally proposed. The buffering effect of capacitance on the magnitude of transpiration-induced xylem tension appears to be coupled to cavitation resistance, possibly alleviating safety versus efficiency trade-offs.

Key-words: capacitance; ecological wood anatomy; hydraulic limits to tree height; Murray's law; safety versus efficiency; vascular design; xylem structure and function; xylem vessel taper.

INTRODUCTION

The concept that the conductance of the hydraulic pathway can constrain the transpiration rate via tension-induced stomatal closure is as old as the cohesion–tension theory (Dixon 1914, chapter 6). Through this link, a plant's hydraulic architecture can influence its CO₂ uptake and

productivity (Brodribb & Hill 1999; Hubbard, Bond & Ryan 1999; Hubbard *et al.* 2001; Brodribb, Holbrook & Gutierrez 2002). The determinants of xylem conductance at the tissue scale have received much attention in relation to the constraints imposed by mechanical safety and resistance to sap cavitation (Hargrave *et al.* 1994; Hacke *et al.* 2001; Domec & Gartner 2002; Cavender-Bares 2005; Sperry, Hacke & Pittermann 2006). Similarly, whole-plant conductance has been analysed in relation to size-dependent constraints on productivity (Ryan & Yoder 1997; Meinzer, Clearwater & Goldstein 2001; Mencuccini 2002; Koch *et al.* 2004) and underlying optimality theory (Becker, Gribben & Lim 2000; Enquist, West & Brown 2000; Niklas & Spatz 2004; McCulloh & Sperry 2005b; Weitz, Ogle & Horn 2006). But a gap exists between the anatomical details of xylem function and its often-simplified representation at the whole-tree scale.

We target this gap in this review, focusing on bridging these two scales towards a more comprehensive understanding. After briefly reviewing the trade-offs at the tissue scale, we provide a fairly explicit framework for incorporating anatomical realism into theory. In a more conceptual vein, we extend the theory to explore the allometry of conductance and volume growth with height, before briefly commenting on the biomechanical versus hydraulic limitations. We conclude with a more descriptive discussion of hydraulic capacitance and its buffering effect on hydraulic constraints. A secondary theme is the contrast between conifers and angiosperms, which successfully support and supply their crowns with a fundamentally different wood structure.

Safety versus efficiency trade-offs at the tissue scale

Efficiency at the tissue scale can be defined as the hydraulic conductivity (volume flow rate per pressure gradient) per fixed cross-sectional area. The area represents the vascular investment per unit length. Conceptually, the conductivity of a given area is maximized by filling it with the fewest, and therefore widest, possible conduits that are also as long as possible and free of internal obstructions. Constraints on the maximum diameter of the conduits, their length and their number per cross-sectional area limit efficiency.

The magnitude of these constraints can be illustrated with a well-known observation (Baas 1986): the number of

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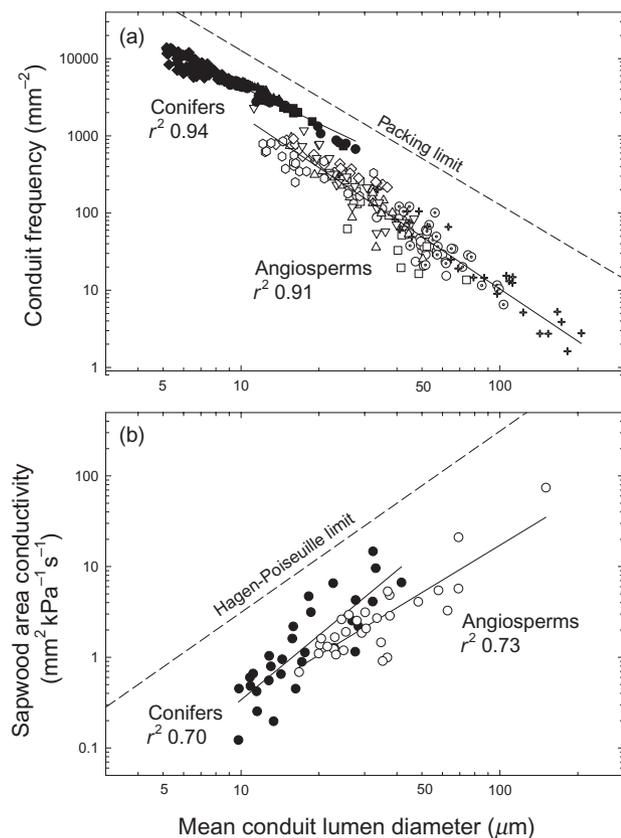


Figure 1. The relationship between (a) conduit frequency (number per wood area) and sapwood conductivity (b) and the average conduit diameter for conifers and angiosperms. (a) Dashed 'packing limit' assumes that all the wood is occupied by conduit lumens of the average diameter. It is within 5% of the actual limit for a normal conduit diameter distribution, with a 20% coefficient of variation. Data are unpublished from multiple saplings and adults of four conifer species (●, *Tsuga heterophylla*; ■, *Pseudotsuga menziesii*; ▲, *Thuja plicata*; ◆, *Abies concolor*), multiple saplings of six angiosperms (○, *Anacardium excelsum*; □, *Luehea seemanii*; △, *Cordia alliodora*; ◇, *Ficus insipida*; ◇, *Acer negundo*; ○, *Alnus rubra*), and adults of these species plus seven others (+, *Vochysia ferruginea*, *Aspidosperma cruenta*, *Tapirira guianensis*, *Tachigalia* sp., *Cecropia longipes*, *Cecropia insignis*). (b) Dashed line is the conductivity per lumen area for an ideal capillary based on the Hagen–Poiseuille equation. (From Sperry *et al.* 2006.)

conduits per wood area (frequency) decreases as their average lumen diameter increases (Fig. 1a, data from trees). This trend implies a constraint on conduit frequency, which is always less than the maximum for wood composed entirely of conduit lumens (Fig. 1a, dashed 'packing limit'). The constraint is much greater for angiosperms because their conduit frequency falls further below the maximum than in conifers. The regressions indicate that vessel lumens occupy only about 8% of the cross-sectional wood area at the mid-point of their diameter range versus 41% for tracheid lumens. Mechanical safety is a clear component of this constraint and it is more important for angiosperms

because they rely on fibres for providing wood strength, whereas conifer tracheids function both in transport and support. In this element of the efficiency versus safety trade-off, conifer xylem is superior to angiosperm xylem.

Conduit diameter and frequency alone do not determine the hydraulic conductivity per cross-sectional area because the conductivity of conduits of a given diameter can vary. The Hagen–Poiseuille equation gives the theoretical maximum, and it seems accurate for vessel lumens with simple perforation plates (Zwieniecki, Melcher & Holbrook 2001). Actual conductivity is less because of scalariform perforation plates and conduit end walls (Ewers 1985; Schulte & Castle 1993; Ellerby & Ennos 1998). Although conduits can theoretically be long enough to eliminate an end-wall effect, they are not. End walls appear to reduce conductivity at a given diameter by a relatively constant 64% in conifers and 56% in angiosperms (with simple perforation plates; Sperry *et al.* 2006). These percentages are remarkably similar considering that tracheids are about 10 times shorter per diameter than vessels and would experience over 95% reduction in conductivity if they had the same end-wall resistance as vessels (Pittermann *et al.* 2006a). The much lower resistance of the inter-tracheid pitting in conifers has been attributed to their specialized torus-margo pit membrane (Pittermann *et al.* 2005).

Because of the relatively similar conductivity per diameter of tracheids and vessels, the greater frequency of tracheids translates into a greater hydraulic conductivity per wood area for a given mean conduit diameter (Fig. 1b). This superiority may help conifers compete with angiosperms, particularly under conditions that limit the diameter of angiosperm vessels to the narrower tracheid range (Pittermann *et al.* 2005).

Although conifer wood is more efficient than angiosperm wood per conduit diameter and length, vessels achieve greater dimensions than tracheids, which can ultimately compensate for these deficiencies and provide greater conductivity per wood area (Fig. 1b). Tracheids undergo little intrusive growth, and their length is limited to a little more than that of their cambial initial (Siau 1971). A tracheid length constraint such as this may explain the 64% end-wall effect: this is similar to the theoretical value of 67% that maximizes the conducting efficiency for a fixed conduit length (Pittermann *et al.* 2006a).

Tracheid diameter is also potentially constrained by hydraulic safety considerations. The danger of freezing-induced cavitation increases dramatically as the mean diameter exceeds approximately 30 μm (Pittermann & Sperry 2006). But this appears to be equally true for vessels (Davis, Sperry & Hacke 1999; Pittermann & Sperry 2003), and it is one factor that can limit vessel diameters to within the tracheid range.

Mechanical safety may pose the strictest limit on tracheid lumen diameter (Jagels *et al.* 2003; Pittermann *et al.* 2006b). Conduits of any type have to be strong enough to avoid imploding by negative sap pressure and also bear any stresses imposed by gravity or the environment on the plant body. A priori, tracheids in wood need to be stronger

than vessels because they double as load-bearing cells. To a first approximation, the strength of the conduit is proportional to how thick the wall is relative to the lumen diameter ('thickness-to-span' ratio; Hacke *et al.* 2001). As expected, tracheids generally have greater thickness-to-span ratios than vessels (Hacke, Sperry & Pittermann 2004).

Greater thickness-to-span ratio is achieved more by a narrowing of the lumen diameter rather than an increase in wall thickness (Pittermann *et al.* 2006b), presumably because of the developmental limits on how thick a wall can grow in its allotted time. In this way, a limit on wall thickness translates into a limit on lumen diameter and conducting efficiency. Thus, tracheids must be narrower than vessels because they must be stronger and have a greater thickness-to-span ratio than vessels. Consistent with this, tracheids are wider in roots than in stems because of reduced mechanical demands, and tracheids tend to be narrower in arid-adapted conifers that need to transport water under more negative pressures (Hacke *et al.* 2001, 2004; Pittermann *et al.* 2006b).

Vessels, although achieving wider diameters and greater lengths than tracheids, also appear to be limited to less than about 0.5 mm in width (Zimmermann 1983), and they are short enough that end walls significantly reduce their efficiency (Wheeler *et al.* 2005). Mechanical constraints on vessel size are probably important, but likely in a more complex manner than in tracheids because of the contributions of fibres to wood and conduit strength (Jacobsen *et al.* 2005).

A major constraint on vessel size may be the safety from cavitation by water stress. Safety depends, in part, on the tightness of the capillary seal that prevents air from leaking across inter-vessel pit membranes (Jarbeau, Ewers & Davis 1995). It only takes one large hole or weak spot in one membrane to disrupt this seal and cause an air seeding of cavitation. According to the pit area hypothesis, the probability of the seal becoming weaker increases as the total area of the pits increases (Wheeler *et al.* 2005). This translates into a complex and variable trade-off between vessel size and vulnerability to cavitation by water stress (Hacke *et al.* 2006).

The torus-margo pits of conifer tracheids have a different mode of sealing that apparently renders them immune to the pit-area mechanism. As a result, there is no evidence that a smaller tracheid is required to increase protection from air seeding in conifers. Instead, there appears to be a trade-off in the structure of the individual pit (Domec, Lachenbruch & Meinzer 2006; Pittermann *et al.* 2006a). Torus-margo pits with tighter seals tend to have lower hydraulic conductance. A tighter seal of the torus over the pit aperture may require a torus that is relatively larger than the aperture. This can be achieved by either reducing the aperture size or increasing the torus – either of which will reduce hydraulic conductance (Domec *et al.* 2006). Furthermore, a stronger and less conductive margo may be required to better hold the torus in position (Hacke *et al.* 2004).

The tree scale

At the scale of the whole-tree vascular system, efficiency can be defined as the hydraulic conductance (volume flow rate per pressure drop) per fixed vascular volume. For a given branching pattern with fixed branch lengths, the most efficient plumbing appears to be a single branched tube that tapers from wide at the trunk to narrow at the tips according to Murray's law (Murray 1926). At this optimal taper, the sum of the tube diameters cubed is equal at all branching levels from trunk to tip. This approximates the architecture of the cardiovascular system.

Xylem networks do not match the peak efficiency of the single branched tube with a Murray taper (McCulloh, Sperry & Adler 2003). The xylem has multiple tubes (conduits) in parallel and in series at every level of branching. Multiple conduits in parallel reduce efficiency over the single branched pipe because they reduce the pipe diameter for the same total vascular volume. Fewer, wide conduits are better than more small ones because of the fourth-power relationship between diameter and conductivity. Multiple conduits in series, instead of one long conduit, reduce efficiency because they force fluid to leave one conduit and enter another by passing through high-resistance end walls. The safety constraints summarized in the previous section are a major reason why xylem conduits are narrower, shorter and more numerous than what would maximize hydraulic conductance per vascular investment.

Murray's analysis of network efficiency has been modified to account for the different structure of the xylem (McCulloh, Sperry & Adler 2004; McCulloh & Sperry 2005a,b, 2006). The only variable in Murray's original problem was how the diameter of the aorta changes as it ramifies to form a network of a given size and volume. We call this the 'diameter ratio' (D_R), which is the distal/proximal diameter across adjacent branch ranks. For xylem, there is an additional variable: how the number of conduits changes across branch ranks. For the multiple parallel/series tubes of a xylem network, this 'number ratio' (N_R) is free to vary: if the trunk has 10 parallel tubes, two daughter branches can have any number greater or equal to 1 each. The number ratio (N_R) is defined as the distal/proximal number of conduits across adjacent ranks.

The efficiency of a xylem network with any number ratio and diameter ratio can be mapped as its conductance for a fixed vascular volume distributed through the network (Fig. 2; McCulloh & Sperry 2005b). In this calculation, the lengths and numbers of the network branches are fixed, as is the number of conduits per terminal branch (Appendix). Because the length is fixed, the network conductance is equivalent to the series conductivity of each branching level from trunk to twig (Eqn A6).

When the number ratio is fixed for a xylem network of fixed volume, as in Murray's original cardiovascular problem, xylem efficiency peaks at the Murray taper that conserves the sum of the conduit diameters cubed (Fig. 2, dashed ML line, $N_R = D_R^{-3}$). Note that there is a corresponding optimal number ratio that maximizes efficiency

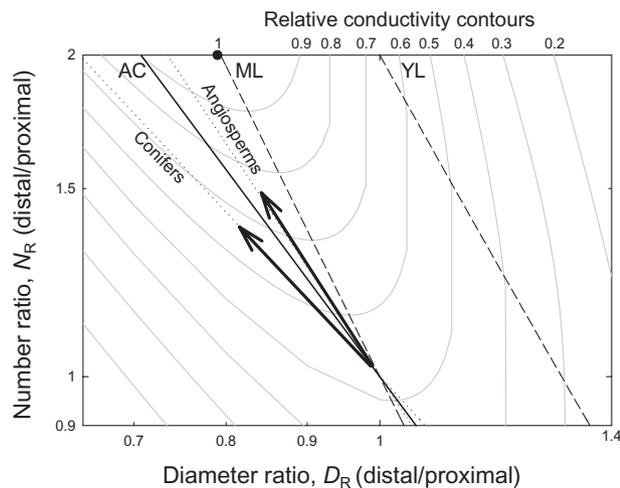


Figure 2. Network conductivity (grey contour lines, relative values labelled on the upper axis) as a function of the distal-to-proximal ratio of the conduit number and conduit diameter. Dashed ‘ML’ line is Murray’s law, where conductivity is maximized for a given number ratio. A bifurcating cardiovascular system has a number ratio of 2 and a maximum efficiency for a diameter ratio of 0.79 (solid symbol). The dashed ‘YL’ line is the so-called ‘Yarrum’s law’: the number ratio that maximizes the conductivity for a given diameter ratio. The solid AC diagonal corresponds to networks with the constant cross-sectional area of conduits summed across each branching level. Networks above the line are top-heavy and increase in area with height. Dotted diagonal lines correspond to the angiosperm and conifer regression slopes from Fig. 1a, assuming a constant cross-sectional area of wood with branch rank. Solid arrows indicate that the diameter ratios are less than 1 and number ratios are greater than 1, which increases the efficiency of the tree hydraulic architecture.

for a given diameter ratio (Fig. 2, dashed YL line); an observation we whimsically call ‘Yarrum’s law’, being a mirror image of Murray’s law. These optima define a ridge of increasing efficiency as the diameter ratio decreases and the number ratio rises to the unattainable maximum for a cardiovascular-type system. Vascular networks of non-woody plants or leaves where the xylem does not have a major mechanical support function tend to track the ridge of maximum efficiency along the Murray law line. But the networks of woody plants, especially trees, fall short (McCulloh *et al.* 2003, 2004).

The need for mechanical stability is a major constraint that keeps woody plant networks off the efficient high ground. To be stable, a tree should not be top-heavy. But the most hydraulically efficient ridgeline networks are top-heavy because the cross-sectional area of the conduits increases from trunk to twig (Fig. 2, conductivity contours above the AC line denoting a constant cross-sectional area across ranks). Mechanical safety trumps hydraulic efficiency because trees maintain an approximately constant cross-sectional area of wood with branching level, at least within their crowns (Enquist *et al.* 2000; Horn 2000). This necessarily limits the cross-sectional area of the xylem conduits, restricting the potential efficiency of the conduit network.

Given the approximately area-preserving branching of woody plants, the universal trend for conduit frequency to decrease with increasing conduit diameter can be used to position trees on the efficiency map. The N_R must equal D_R^c , where c is the slope of the log–log relationship in Fig. 1a between conduit frequency and diameter (Fig. 2, dotted angiosperm and conifer lines; Eqn A7). Within an individual, the trend results from conduits becoming narrower and more numerous per xylem area moving from trunk to twig. On the efficiency map, this means that $N_R > 1$ and $D_R < 1$. This trend is adaptive because it moves the network to higher efficiency along the sidehill route near the constant area line (Fig. 2, arrows). How high the efficiency climbs depends on how much the diameter tapers across branch ranks. This reinforces the advantages of the diameter taper for promoting hydraulic segmentation (Zimmermann 1978), for minimizing the differences in conductance to leaves throughout the crown and minimizing the hydraulic penalties of height growth (Becker *et al.* 2000; Enquist *et al.* 2000), and for maintaining the safety margins from cavitation and mechanical failure with height (Sperry & Saliendra 1994; Domec & Gartner 2002; Burgess, Pittermann & Dawson 2006).

Looking more closely, the angiosperm trend shows a tendency towards area-increasing branching of their vessel network within the area-preserving branching of the plant as a whole (Fig. 2, angiosperm arrow above AC line). This is also evident from the tendency of narrower vessels to occupy proportionately more of the available wood area than wider vessels (Fig. 1a). This promotes greater efficiency of the conduit network than the conifer trend towards area-decreasing conduit branching (Fig. 2, conifer arrow below AC line); a trend also evident from narrower tracheids occupying less of the possible area than wide ones (Fig. 1a). This trend is consistent with narrow tracheids having higher thickness-to-span ratio than wide ones, possibly in response to greater mechanical demands including the support of more negative sap pressures (see previous section).

The network efficiency map (Fig. 2) represents conductance for a fixed volume of conduits. It does not account for efficiency on the basis of added tissue volume for mechanical support and other functions. Efficiencies per fixed wood volume are much lower (Fig. 3; Eqns A8 & A9). A tracheid lumen volume that is 41% of the total wood volume (from Fig. 1a) decreases conifer efficiency by 83% for a given diameter ratio (Fig. 3, compare conifer curves; Eqn A9). An angiosperm vessel volume of only 8% of the wood volume drops efficiency by over 99% (not shown).

As mentioned, angiosperms can compensate for their lower vessel frequencies by achieving greater conduit diameters than conifers. In the network efficiency calculation, the conduit diameter range across the branch ranks is determined by the number of conduits per terminal branch (Eqn A5 & A5a). The lower this constant, the wider the conduits throughout the network. In the network comparisons so far, this number was fixed. In truth, it varies considerably – particularly between conifers and angiosperms.

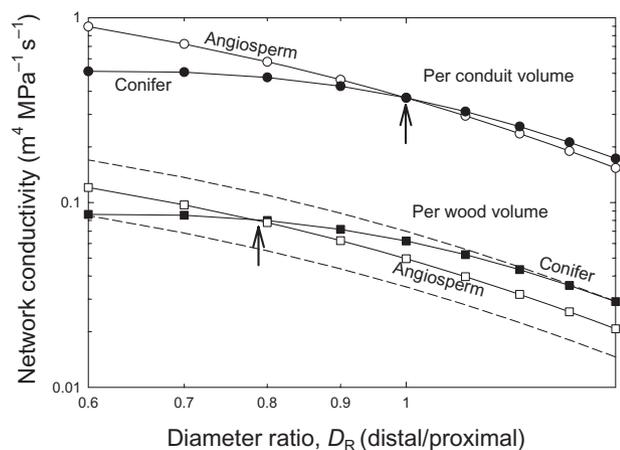


Figure 3. Network conductivity of angiosperms and conifers as a function of conduit diameter ratio, assuming the dotted-line trajectories on the efficiency map of Fig. 2. Upper curves are the efficiency per fixed conduit volume: the same conductivity profile along the dotted angiosperm and conifer lines in Fig. 2. Angiosperms have greater efficiency for diameter ratios less than 1 (arrow). The lower curves are the efficiency per fixed wood volume, where conduit volume is 41% of the total in conifers and 8% of the total in angiosperms, consistent with Fig. 1a. The angiosperm curve is further adjusted to account for fewer, wider conduits per terminal branch as compared with conifers, also consistent with Fig. 1a. The crossover point where angiosperm efficiency exceeds that of conifers (arrow) depends on the number, and hence the diameter, of conduits per terminal branch, shifting the efficiency as indicated by the dashed lines. Conductivity values are arbitrary, but not the relationships between the curves.

This is evident from the intra-specific data in Fig. 1a: the twig tracheids of conifer species are much more numerous and narrow than the twig vessels of angiosperm species.

Adjusting the angiosperm network accordingly, and increasing vessel diameters by two- to threefold relative to tracheids, causes the angiosperm efficiency to rise to the conifer range (Fig. 3, angiosperm curves for total wood volume). The range of vessel diameters is about two to eight times that of tracheids (Fig. 1), suggesting that angiosperms can reach and, in some cases, exceed the efficiency of conifer networks (Becker, Tyree & Tsuda 1999). Which network is superior depends on the relative volume fractions of conduits, their diameter ranges and the diameter ratio within the network (Fig. 3). These parameters in turn are constrained, in part, by the hydraulic and mechanical demands placed on the wood at the tissue scale.

The considerable overlap in hydraulic efficiency of conifer and angiosperm woods is expected, given the clear success of both wood types. Conifers appear superior when safety trade-offs with freezing and water stress limit vessels to a narrow diameter range; angiosperms have superior efficiency when these safety constraints are relaxed and vessel diameters increase.

The hydraulic architecture theory we have outlined was inspired by the pioneering work of West, Brown and Enquist (WBE; West, Brown & Enquist 1997; Enquist *et al.*

2000), but it differs in being more anatomically flexible and realistic. Their architecture assumes that $N_R = 1$ within a growth increment, and that $N_R < 1$ for the tree as a whole. In combination with their assumptions of an area-preserving branching and conduit taper, conduits become narrower and fewer per area going from trunk to twig. This is the opposite of what is observed (a positive rather than a negative slope in Fig. 1a). The prediction of the wrong diameter versus frequency relationship requires modifications to the otherwise very influential WBE approach.

Tree hydraulics and ontogeny: implications for height growth

The efficiency analysis presented in Fig. 2 is independent of size and length, showing the advantages of conduits becoming wider and less frequent from twig to trunk for increasing the conductance for a fixed investment in the vascular volume. In a growing tree, this fixed volume would represent an annual growth increment. As a tree grows, this architecture also determines how conductance scales with height, a topic basic to whether water supply limits height growth (Ryan & Yoder 1997; Ryan, Phillips & Bond 2006).

There is an inescapable hydraulic consequence of growing tall: the volume of vascular tissue required to support and supply an ever-taller tree increases more than the hydraulic conductance of the tissue. This is because tissue volume (V) increases with its cross-sectional area (A) times height (H ; $V \propto AH$), whereas hydraulic conductance (K) for conduits with no taper increases with cross-sectional area divided by height ($K \propto AH^{-1}$; Eqns A10 & A11). Taper reduces the dependence of conductance on height, but cannot eliminate it entirely. Calculations based on the diameter versus frequency relationships in Fig. 1a indicate that the maximum effect of the taper is to make $K \propto AH^{-0.35}$ (Appendix). These trends are illustrated in Fig. 4a for $A \propto H^3$, which assumes the typical scaling of the basal diameter increasing with length to the 1.5 power as required for a constant safety margin from Euler buckling (McMahon 1973). Tissue volume, in this example, will increase with height to the fourth power (Fig. 4a, volume curve), whereas conductance increases with height to the second power without a taper, and 2.65 power with a maximum taper (Fig. 4a, lower and upper conductance curves). But no matter what A -by- H scaling is adopted, the conclusion stands that vascular conductance cannot keep pace with vascular volume during length growth.

According to the 'hydraulic limitation hypothesis' (HLH), this robust pattern is non-sustainable and leads to a limit on tree height. The hypothesis is a matter of much debate (Ryan *et al.* 2006), and here we only define the influence of architectural patterns on its formulation. The original concept was based on a carbon-budget argument, which we may explain somewhat differently here. If tree photosynthesis is some function of tree conductance, it will be, in turn, some function of AH^{-b} , where b is somewhere between 1 and 0.35 depending on the taper as discussed earlier. If tree respiration is a function of xylem volume, it

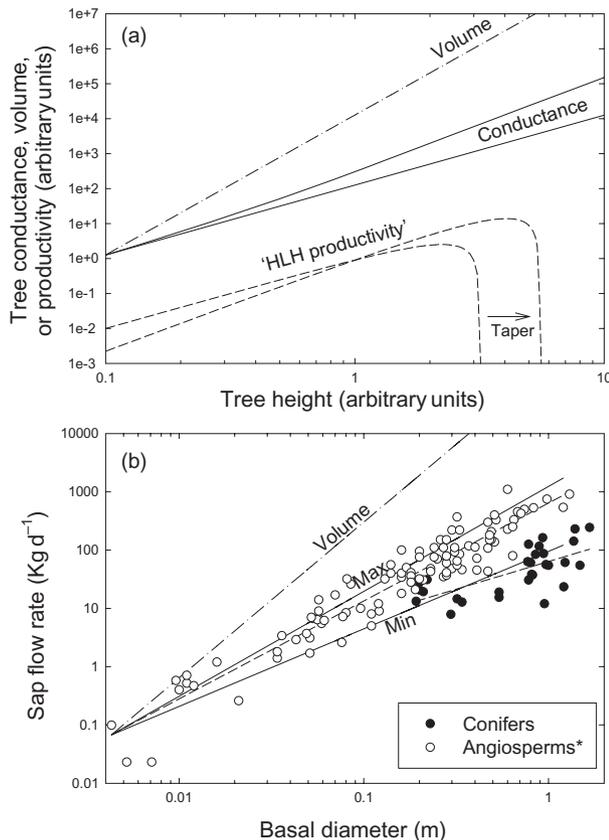


Figure 4. Scaling of tree stem volume, conductance and potential productivity with height (a) and scaling of daily sap flow volume with the basal diameter (b). (a) Allometry assumes a basal diameter proportional to height to the 1.5 power, and a collective branch area constant with height. Volume scales with height to the fourth power (dash-dotted). The upper solid conductance curve corresponds to the angiosperm vessel diameter versus frequency relationship in Fig. 1a and assumes a 20-fold increase in vessel diameter from twig to trunk: conductance increases with height to the 2.65 power. The lower solid line is for a constant vessel diameter and the scaling exponent is 2. Dashed 'HLH productivity' lines illustrate the original hydraulic limitation hypothesis (HLH). They are calculated from the scaling of the conductance and volume and indicate the potential for trees to reach their compensation point at a theoretical height. The arrow indicates the advantage of the conduit taper for minimizing this limitation. (b) Scaling of sap flow with the basal diameter for two data sets (Enquist *et al.* 2000; Meinzer *et al.* 2005) of predominately self-supporting angiosperms (open circles, dashed line is pooled OLS regression) and one data set of conifer trees (solid circles; Meinzer *et al.* 2005). 'Max' and 'min' lines correspond to the conductance curves in (a). Dash-dotted 'volume' line indicates a sap flow proportional to tree volume.

will, in turn, be related to AH . Tree productivity, photosynthesis minus respiration, will be some function of $(AH^{-b} - AH)$. This term increases with H to a plateau before plummeting to zero, indicating the potential of this scaling to force the tree to its compensation point at a maximum height. Just to illustrate the relevance of the conduit taper, we insert an allometric constant, 'k', to represent the

relative scaling of respiration and photosynthesis so that the rate of potential biomass production becomes proportional to $(AH^{-b} - kAH)$, as shown in Fig. 4a (dashed 'HLH productivity' curves). Although a vast oversimplification, this illustrates the ability of the taper to minimize (but not eliminate) any hydraulic limitation on productivity with height (Fig. 4a, 'taper' arrow). Importantly, whether the A represents total basal area, sapwood area or just the outermost annual ring, this pattern is the same.

Although simple in concept, the HLH is complex in reality because of the many variables involved in linking tree photosynthesis and respiration with the allometry of xylem conductance and volume with height. Evidence that tall trees do not become progressively more carbon limited suggests that other factors may be paramount (Ryan *et al.* 2006). Productivity may be less limiting than height-related reductions in cell turgor and expansion rate (Koch *et al.* 2004; Woodruff, Bond & Meinzer 2004). But the scaling of tree conductance with volume could also constrain the expansion of growing tissues, an idea we return to later.

The effect of the conduit taper ($D_R < 1$) on tree conductance depends on how the number of conduits changes (N_R). This point is neglected in the rapidly proliferating literature on taper (Enquist *et al.* 2000; Zaehle 2005; Anfollilo *et al.* 2006; Weitz *et al.* 2006; Mencuccini *et al.* 2007). Taper can make the overall hydraulic conductance of a single file of conduits independent of height because the conductance is limited by the narrowest conduits in a single file. If the total number of parallel conduits in the growth increment is either equal with height ($N_R = 1$), or becomes less with height ($N_R < 1$), as in the WBE architecture, tree conductance can increase in proportion to the basal area and otherwise be independent of height. In Fig. 4a, the conductance scaling exponent would be 3 rather than 2.65. The lower exponent of 2.65 represents real trees, where $N_R > 1$; a more optimal pattern that improves their conductance per growth investment relative to $N_R < 1$ (Fig. 2). When $N_R > 1$, there are always multiple narrow conduits in parallel for a single wide trunk conduit, and so the narrow conduits are less limiting to the total conductance of the growth increment. As a result, even with the taper, the whole-tree conductance is dependent on height (Mencuccini & Magnani 2000; Zaehle 2005). Adding leaves to the flow path should not materially alter this conclusion because leaf vasculature appears to continue (and amplify) the $D_R < 1$ and $N_R > 1$ trend in stems (McCulloh *et al.* 2003).

Actual trees fall between the best- and worst-case scenarios for conductance trajectories in Fig. 4a. Mencuccini's meta-analysis (2002; also Mencuccini & Magnani 2000) found that whole-tree conductance was proportional to the basal diameter raised to a scaling exponent averaging 1.49 (range: 1.23–1.72) for two angiosperms and two conifers. For basal diameter scaling with height to the 1.5 power (McMahon 1973), conductance would scale with height to the $1.49 \times 1.5 = 2.24$ power, which is between the 2 and 2.65 power scaling for conductance in Fig. 4a. Mencuccini (2003) also found that whole-plant conductance increased with plant mass to a common scaling exponent of 0.58 power,

consistent with the 0.5 (no taper) to 0.66 (maximum) range for the conductance versus volume proportionalities shown in Fig. 4a. These observations are not consistent with conductance (and its influence on volume flow rate or productivity), scaling with mass to the 0.75 power, as would be the case for the WBE architecture (Enquist *et al.* 2000).

Sap flow data are similarly consistent with the conductance curves in Fig. 4a. Whole-tree volume flow rate should scale with whole-tree conductance if the flow-induced pressure drop is independent of height. If so, the scaling of conductance with height (Fig. 4a) should bound the scaling of sap flow with height. The sap flow data in Fig. 4b were reported per stem basal diameter. Assuming again that the basal diameter scales with height to the 1.5 power, tree conductance should scale with basal diameter to the 1.8 power at a maximum and 1.33 at a minimum (Fig. 4b, max and min slopes). These limits roughly define the range of observed sap flow scaling for angiosperm and conifer data sets (Fig. 4b, symbols, dashed regression lines).

Trade-offs between safety and efficiency may have their greatest relevance for height growth by limiting hydraulic conductance at the top of the tree. A consequence of conduit tapering is that the absolute value of tree conductance will be highly influenced by the terminal branches and leaves. If the conductance of the terminal units became lower with height because of greater safety requirements, it could prevent an exponential increase in conductance. A flatter increase in conductance with height may explain the tendency for an arguably sigmoidal rather than exponential increase in sap flow with tree size in Fig. 4b (Meinzer *et al.* 2005). This would greatly amplify any hydraulic penalty associated with height growth.

In Douglas fir, one of the world's tallest tree species, height-related increases in resistance to xylem embolism were associated with an exponential increase in xylem-specific resistivity (Fig. 5). The vertical trends in xylem safety and efficiency were determined largely by a bordered pit structure (Domec *et al.* 2006). Increasing resistance to embolism by air seeding was associated with a steeper vertical decline in pit aperture diameter than in torus diameter, resulting in a greater torus overlap of the aperture and, therefore, more reliable sealing of the aperture during pit aspiration (Domec *et al.* 2006). But the smaller apertures contributed to the vertical decline in xylem efficiency. These results suggest that the vertical scaling of the tracheid structure related to safety issues may limit the conducting capacity of the twigs, and influence the maximum height of Douglas fir trees.

One way around the hydraulic constraint on growth rate is for the plant to drop its leaf xylem pressure with height so that water transport increases at the same pace as volume growth. Although a drop in midday xylem pressure with height is often observed across trees (McDowell *et al.* 2002; Koch & Fredeen 2005; Woodruff *et al.* 2007), it is not nearly on the scale required for water transport to scale isometrically with volume. Otherwise, sap flow would scale with the stem diameter to the 2.67 power, which is far from observation (Fig. 4b, volume slope). The obvious problem is that

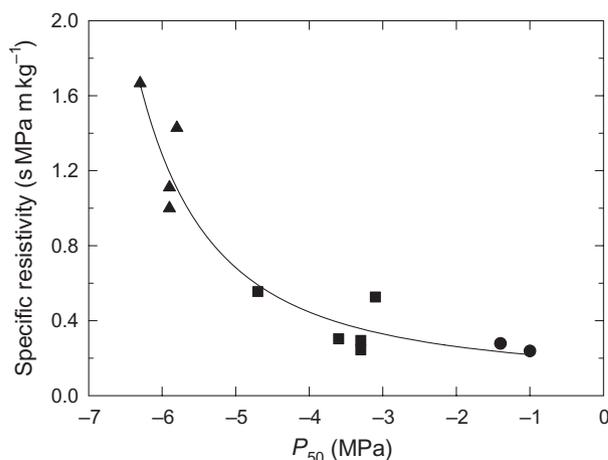


Figure 5. Relationship between the efficiency and safety of the Douglas fir xylem along a 42 m height gradient that includes roots (●), trunks (■) and branches (▲). Xylem resistivity and, therefore, the axial tension gradient at constant flux increase exponentially as resistance to embolism increases from the roots to the upper branches. (Data taken from Domec *et al.* 2006.)

such low xylem pressures would have negative consequences for inducing cavitation, slowing cell expansion and other responses to water stress, so that one problem is traded for a much worse alternative.

The possibility that constraints on cell expansion are more limiting than productivity for height growth may have important links to hydraulic architecture. Height-related reductions in shoot expansion and cell size in Douglas fir, coast redwood and other conifers appear to be governed largely by the vertical gradients of declining turgor during the short, but critical, period of expansive growth during the late spring, when the rate of osmotic adjustment is not sufficient to compensate for the vertical hydrostatic gradient (Woodruff *et al.* 2004; Meinzer, Bond & Karanian 2008b). Turgor is not the only biophysical determinant of cell expansion, but measurements on expanding Douglas fir shoots yielded no evidence of vertical trends in either tissue plastic extensibility or the yield threshold for growth that would be consistent with reduced tissue expansion (Meinzer *et al.* 2008b).

Hydraulic conductance to growing tissue also constrains cell expansion independently of turgor and yield thresholds (Cosgrove 1997). An intriguing alternative to the original carbon balance argument for a hydraulic limitation is that the progressive reduction in hydraulic conductance per volume of growing tissue with height (Fig. 4a) may act to limit tissue growth together with the gravity gradient. In turn, limited cell expansion could reduce the size of the distal-most xylem conduits, feeding back to create a greater hydraulic limitation. Thus, the inherent constraints on physiological processes such as osmotic adjustment and cell expansion may have important feedbacks on the xylem structure and hydraulic architecture at multiple scales.

Mechanical versus hydraulic constraints

The concepts underlying a hydraulic limit on height growth also relate to the constraints on radial growth. For trees with secondary growth, the typical scaling of stem diameter with height to the $x = 1.5$ power maintains a constant safety margin from Euler buckling. A smaller exponent (the minimum being $x = 0$) leads to a mechanical limit to height growth; a larger one leads to an increasing mechanical safety with height, and lower height growth per volume increment (King 1990). From the hydraulic standpoint, x in theory should not influence the potential hydraulic constraint on productivity or growth because it only influences the common area term (A) in the ($AH^{-b} - AH$) trade-off. However, smaller x translates into greater height growth rate for a given productivity: relatively skinny stems (small x) will grow faster in length than fat stems. Circumstances favouring rapid length growth would result in x values well below 1.5.

This suggests that $x = 1.5$ results much more from a mechanical constraint than a hydraulic one, contradicting the analysis of Niklas & Spatz (2004), but consistent with other studies finding a pre-eminent mechanical constraint (Taneda & Tateno 2004). The simplest test of Niklas and Spatz's conclusion is whether the diameter versus length relationship for vines gives $x = 1.5$. It should, if hydraulics is limiting, but x should be less than 1.5 if mechanical safety is paramount. Allometric data is less abundant for vines than trees, but consistently indicate an x much less than 1.5, closer to $x = 0.5$ (Niklas 1994).

Capacitance

The hydraulic capacitance (C) of xylem is a key functional trait that modulates the compromise between xylem safety and efficiency under the dynamic conditions that prevail in intact plants. During the day, xylem water flux and, consequently, tension are rarely at steady state owing to the continual fluctuations in atmospheric evaporative demand and stomatal conductance. Transient, transpiration-induced increases in xylem tension result in the capacitive discharge of water into the transpiration stream, effectively bypassing a portion of the soil-to-leaf hydraulic resistance and lengthening the time required for tension and flow to attain steady-state values throughout the plant (e.g. Williams *et al.* 1996; Phillips *et al.* 1997, 2004). Thus, caution should be exercised in using the hydraulic conductivity of excised root and stem segments measured under quasi-steady-state conditions to infer the axial tension gradients and maximum xylem tensions sustained *in vivo*.

Consistent with an Ohm's law analogue for xylem water transport, the C of a tissue is traditionally defined as the ratio of change in its water content to change in its water potential ($dW/d\psi$). However, for comparisons among species and individuals of different sizes, it is often more informative to express C in terms of the mass of water released per tissue volume per change in water potential (Meinzer *et al.* 2003; Scholz *et al.* 2007), or the total mass of

water withdrawn daily from internal storage per change in water potential between two points in the soil–plant system (Meinzer, James & Goldstein 2004). According to the cohesion–tension theory, a change in transpiration should result in the essentially instantaneous onset of changes in the flow and xylem tension throughout the plant, but in keeping with an electric circuit analogue, C can substantially increase the time constant ($R \times C$) for tension and flow to reach new steady-state values (Phillips *et al.* 1997, 2004; Meinzer *et al.* 2004). Capacitance thus confers elasticity on an otherwise inelastic system.

A variety of tissues can contribute to the total C or internal water storage capacity of plants (Goldstein, Meinzer & Monasterio 1984; Nielsen *et al.* 1990; Holbrook & Sinclair 1992). Here we focus on the role of sapwood C in the hydraulic architecture because in woody plants, the sapwood contains the functional xylem conduits and represents nearly the entire length of the root-to-leaf water transport pathway. Moreover, several studies have reported that the sapwood is the major source of stored water that is withdrawn and recharged on a seasonal (Waring & Running 1978; Waring, Whitehead & Jarvis 1979) and daily basis (e.g. Lo Gullo & Salleo 1992; Loustau *et al.* 1996; Meinzer *et al.* 2003; Čermák *et al.* 2007; Scholz *et al.* 2007). There are notable exceptions to this pattern though (Chapotin, Razanameharizaka & Holbrook 2006a,b).

The intrinsic C of the sapwood varies widely among species. Moisture-release curves determined on angiosperm and conifer sapwood typically yield values of C ranging from 40 to 500 kg m⁻³ MPa⁻¹ (Meinzer *et al.* 2003, 2006, 2008a; Scholz *et al.* 2007). These values are based on the initial, nearly linear portion of the moisture-release curve that comprises the normal physiological operating range of the sapwood water potential *in vivo* (Meinzer *et al.* 2003). As expected, sapwood C generally declines with increasing wood density (Meinzer *et al.* 2003; Scholz *et al.* 2007). However, unlike the universal relationship between the sapwood saturated water content and density (Simpson 1993), the relationship between sapwood C expressed as kg m⁻³ MPa⁻¹ and wood density appears to vary across species and types of xylem (cf. Meinzer *et al.* 2003, 2006; Scholz *et al.* 2007).

Although absolute amounts of water derived from C may constitute only 10–30% of the total daily transpiration (Loustau *et al.* 1996; Goldstein *et al.* 1997; Phillips *et al.* 2003), the buffering impact of C on the daily dynamics of plant–water relations and maximum tensions generated in the terminal portions of the water transport pathway can be substantial, even in relatively small plants with a limited total water storage capacity. Inverse relationships between sapwood C and daily maximum xylem tension exist across a range of species. In tropical forest canopy trees, the daily minimum water potential of terminal branches increased linearly from -1.5 to -0.6 MPa with a 300 kg m⁻³ MPa⁻¹ increase in species-specific values of sapwood C (Meinzer *et al.* 2003, 2008a). Even in much smaller 2- to 6-m-tall Brazilian savannah trees, the daily minimum leaf water potential increased by 0.8 MPa over a 120 kg m⁻³ MPa⁻¹ range of

sapwood C (Scholz *et al.* 2007). Similarly, the diurnal variation in leaf water potential decreased by about 0.9 MPa with a 35% increase in sapwood saturated water content (a proxy for C) among 3- to 4-m-tall individuals of six Hawaiian dry forest tree species (Stratton, Goldstein & Meinzer 2000). Thus, under the dynamic flow regimes that prevail in intact plants, capacitance-dependent time constants appear to prevent xylem tension from attaining the maximum values expected from steady-state pressure–flux relationships in the segments of excised xylem.

The preceding relationships suggest that the dampening effect of C on the daily fluctuations in xylem tension may partially mitigate some consequences of the trade-off of xylem safety against efficiency. Results of some recent work provide support for this hypothesis. A positive, linear relationship between the stem xylem water potential at 50% loss of hydraulic conductivity (P_{50}) and sapwood C has been observed among nine species of Rhamnaceae from the California chaparral (Pratt *et al.* 2007) and among 11 tropical forest canopy tree species from Panama (Fig. 6a; Meinzer *et al.* 2008a). Furthermore, vessel implosion resistance declined with increasing stem C among the nine chaparral species (Pratt *et al.* 2007), and among the 11 Panamanian tree species the difference between daily minimum stem water potential and P_{50} , a proxy for the hydraulic safety margin for avoiding runaway embolism, declined with increasing stem C (Fig. 6b; Meinzer *et al.* 2008a). Importantly, there was no significant relationship between P_{50} and stem xylem-specific conductivity in either the chaparral or tropical tree species (Pratt *et al.* 2007; Meinzer *et al.* 2008a). However, stem xylem vulnerability was positively related to both C and xylem-specific conductivity in two conifers, *Pinus ponderosa* (Domec & Gartner 2003) and *Pseudotsuga menziesii* (Domec & Gartner 2001). These results point to a prominent linkage between stem C and the evolution of suites of hydraulic architectural traits. By transiently uncoupling xylem tension from the series of hydraulic resistances upstream, C appears to mitigate the requirements for investment in features that enhance resistance to xylem embolism and implosion.

Recent studies of tropical trees suggest that the stomata regulate transpiration in a manner that optimizes the capacitive discharge of water from stem tissue, while at the same time avoiding excessive embolism. Species-specific set points for the daily minimum water potential of terminal branches appear to represent a compromise that maximizes the reliance on stored water over the range where C is nearly constant as sapwood water deficit increases (Fig. 7a), but minimizes the risk of embolism as both C and its buffering effect diminish beyond this point and embolism begins to increase exponentially (Fig. 7b). Other tropical and temperate tree species appear to exhibit a similar type of coordination between leaf- and stem-water relations that results in set points for the minimum stem water potential corresponding to the transition from a gradual to an exponential increase in embolism with increasing stem water deficit (Brodribb *et al.* 2003; Domec *et al.* 2006). This regulatory behaviour can be interpreted as another

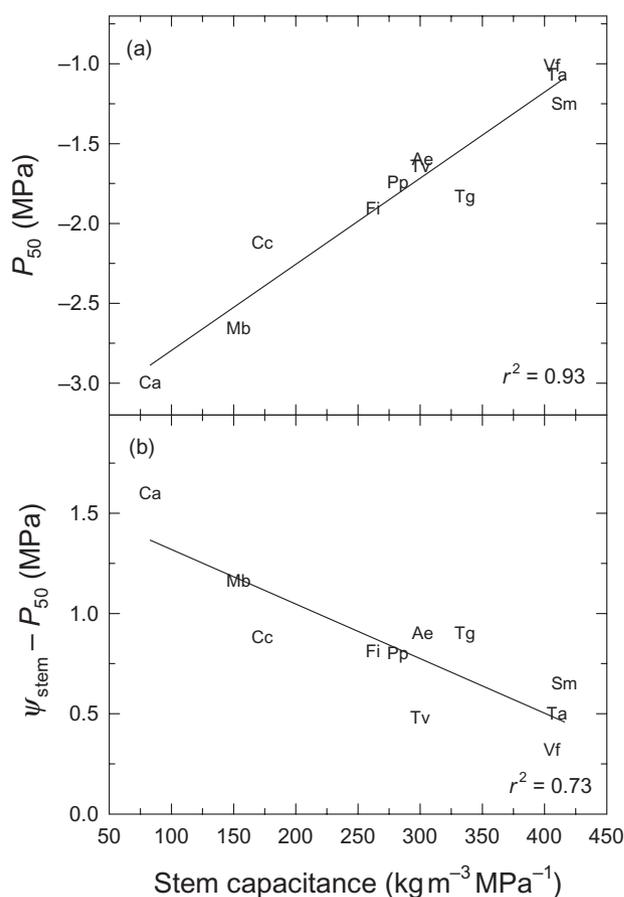


Figure 6. Relationship between stem xylem safety and stem sapwood capacitance for 11 tropical forest tree species. (a) Stem xylem pressure corresponding to 50% loss of maximum hydraulic conductivity (P_{50}). (b) The difference between the daily minimum water potential of intact stems in the field (Ψ_{stem}) and P_{50} , a proxy for the safety margin from runaway embolism. Species abbreviations: Ae, *Anacardium excelsum*; Ca, *Cordia alliodora*; Cc, *Chrysothamnus cainito*; Fi, *Ficus insipida*; Mb, *Manilkara bidentata*; Pp, *Protium panamense*; Sm, *Schefflera morototoni*; Ta, *Trattinnickia aspera*; Tg, *Tapirira guianensis*; Tv, *Tachigalia versicolor*; Vf, *Vochysia ferruginea*. (From Meinzer *et al.* 2008a and Meinzer, unpublished observations.)

manifestation of a compromise between xylem safety and efficiency represented by the contribution of stored water to the transpiration stream, which results in the transient increases in apparent hydraulic conductance. Thus, C is a tissue-level biophysical property with multiple impacts on whole-plant function.

CONCLUSIONS

Although the hydraulic architecture of trees has its complexities, we have chosen to emphasize the strong patterns that propagate from tissue to tree scales. In most cases, we have also been able to provide hypotheses for the constraints and adaptations that underlie these patterns. Mechanical constraints have been proposed at several levels: limiting the area of wood for conduction, limiting

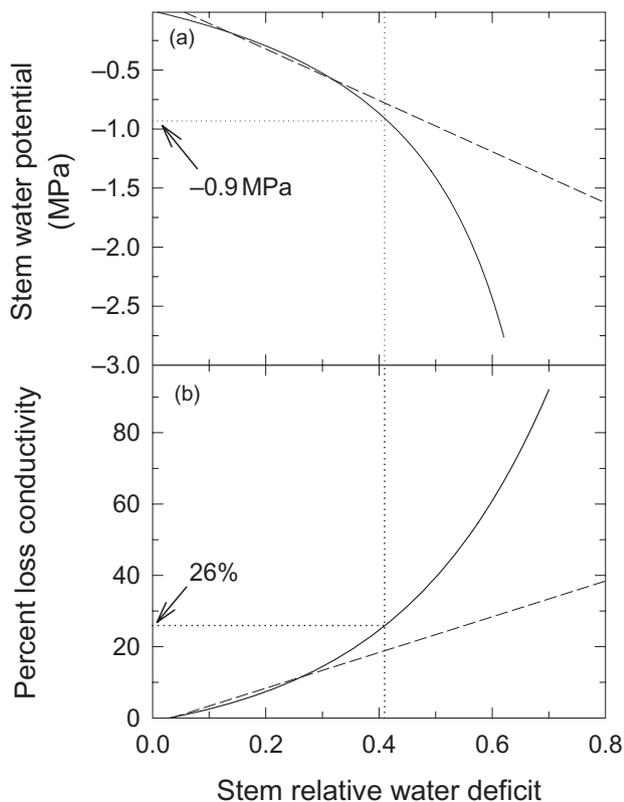


Figure 7. Typical curves showing the dependence of (a) stem water potential and (b) loss of stem hydraulic conductivity on stem relative water deficit for several Panamanian forest tree species. In (a), the minimum water potential observed in intact terminal branches in the field (-0.9 MPa) falls on the portion of the stem moisture-release curve where capacitance begins to decrease sharply with increasing water deficit as indicated by the divergence between the curve and the dashed line. In (b), xylem embolism begins to increase sharply at a value of relative water deficit associated with the minimum water potential corresponding to intact stems. Mean loss of conductivity corresponding to the mean maximum daily relative water deficit was $31 \pm 2\%$ for the eight species examined. Dashed lines represent linear regressions fitted to the initial nearly linear portions of the curves. (Based on data in Meinzer *et al.* 2008a.)

the diameter of conduits – especially tracheids – preventing top-heavy trees that would otherwise be more hydraulically efficient, and forcing trunk diameter to increase with height to the 1.5 power when a lower exponent would maximize the rate of height growth from a hydraulic standpoint. Similarly, hypothetical hydraulic constraints act at various scales: protection from air seeding of cavitation may limit the inter-tracheid pit conduction in conifers and the vessel size in angiosperms; protection from freezing-induced cavitation limits the conduit diameter similarly in both tree types; and hydraulic conductance of trees does not increase sufficiently with height to prevent a potential constraint on height growth.

The frequency versus diameter trend together with area-preserving branching results in trees having more, narrower conduits moving from trunk to leaf ($D_R < 1$, $N_R > 1$). This

strong pattern has many potential advantages. Perhaps, most fundamentally, it tends to maximize the conductance-per-growth increment. It also minimizes the difference in conductance to shoots at the top of the tree versus that at the bottom, promoting a more equable water distribution. It results in steeper pressure gradients distally, which can restrict stress-related dieback to replaceable twigs and leaves as opposed to main branches. At the same time, it places the narrowest and safest conduits where the pressures are lowest.

The adaptive value of capacitance is, at least in part, its buffering of transpirational water stress. Its apparent coupling to cavitation resistance allows maximum water release within the physiological range before extensive cavitation occurs. The tendency for capacitance to decline in more cavitation-resistant species could be a constraint, because traits associated with cavitation resistance such as greater wood density and more rigid walls can also minimize capacitance. But capacitance may also not be as important for these arid-adapted species, which experience long-term monotonic declines in water potential that minimize capacitance's buffering effects.

Although there are some seemingly universal trends in tree architecture, there are variations on the theme that distinguish functional types. The diameter versus frequency trend in Fig. 1a may be universal, but just as conifers and angiosperms have different slopes and intercepts, it is likely that, especially, within angiosperms there are differences between species and wood types. These may reflect the different mechanical constraints and safety versus efficiency compromises. Diffuse- and ring-porous trees would make for an interesting contrast in this regard, as would vines and root systems, with their different mechanical requirements. Also informative would be comparisons across habitats with different transpirational demands. Maximizing the hydraulic efficiency or height growth is less important in shady, nutrient-limited, humid or high- CO_2 habitats than elsewhere. Such comparisons are the natural experiments that can test and advance our interpretation of the biological significance of observed architectural patterns.

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REFERENCES

- Anfodillo T., Carraro V., Carrer M., Fior C. & Rossi S. (2006) Convergent tapering of xylem conduits of different woody species. *New Phytologist* **169**, 279–290.
- Baas P. (1986) Ecological patterns of xylem anatomy. In *On the Economy of Plant Form and Function* (ed. T.J. Givnish), pp. 327–351. Cambridge University Press, Cambridge, UK.
- Becker P., Tyree M.T. & Tsuda M. (1999) Hydraulic conductances of angiosperm versus conifers: similar transport sufficiency at the whole-plant level. *Tree Physiology* **19**, 445–452.

- Becker P., Gribben R.J. & Lim C.M. (2000) Tapered conduits can buffer hydraulic conductance from path-length effects. *Tree Physiology* **20**, 965–967.
- Brodribb T. & Hill R.S. (1999) The importance of xylem constraints in the distribution of conifer species. *New Phytologist* **130**, 365–372.
- Brodribb T.J., Holbrook N.M. & Gutierrez M.V. (2002) Hydraulic and photosynthetic co-ordination in seasonally dry tropical forest trees. *Plant, Cell & Environment* **25**, 1435–1444.
- Brodribb T.J., Holbrook N.M., Edwards T.J. & Gutiérrez M.V. (2003) Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant, Cell & Environment* **26**, 443–450.
- Burgess S.S.O., Pittermann J. & Dawson T.E. (2006) Hydraulic efficiency and safety of branch xylem increases with height in *Sequoia sempervirens* (D. Don) crowns. *Plant, Cell & Environment* **29**, 229–239.
- Cavender-Bares J. (2005) Impacts of freezing on long distance transport in woody plants. In *Vascular Transport in Plants* (eds N.M. Holbrook & M.A. Zwieniecki), pp. 401–424. Academic Press, Amsterdam, the Netherlands.
- Čermák J., Kučera J., Bauerle W.L., Phillips N. & Hinckley T.M. (2007) Tree water storage and its diurnal dynamics related to sap flow and changes in stem volume in old-growth Douglas-fir trees. *Tree Physiology* **27**, 181–198.
- Chapotin S.M., Razanameharizaka J.H. & Holbrook N.M. (2006a) Baobab trees (*Adansonia*) in Madagascar use stored water to flush new leaves but not to support stomatal opening before the rainy season. *New Phytologist* **169**, 549–559.
- Chapotin S.M., Razanameharizaka J.H. & Holbrook N.M. (2006b) Water relations of baobab trees (*Adansonia* L.) during the rainy season: does stem water buffer daily water deficits? *Plant, Cell & Environment* **29**, 1021–1032.
- Cosgrove D.J. (1997) Relaxation in a high stress environment: the molecular bases of extensible cell walls and cell enlargement. *The Plant Cell* **9**, 1031–1041.
- Davis S.D., Sperry J.S. & Hacke U.G. (1999) The relationship between xylem conduit diameter and cavitation caused by freeze-thaw events. *American Journal of Botany* **86**, 1367–1372.
- Dixon H.H. (1914) *Transpiration and the Ascent of Sap*. Macmillan and Co. Ltd, London, UK.
- Domec J.-C. & Gartner B.L. (2001) Cavitation and water storage capacity in bole xylem segments of mature and young Douglas-fir trees. *Trees* **15**, 204–214.
- Domec J.-C. & Gartner B.L. (2002) Age- and position-related changes in hydraulic versus mechanical dysfunction of xylem: inferring the design criteria for Douglas-fir wood structure. *Tree Physiology* **22**, 91–104.
- Domec J.-C. & Gartner B.L. (2003) Relationship between growth rates and xylem hydraulic characteristics in young, mature and old-growth ponderosa pine trees. *Plant, Cell & Environment* **26**, 471–483.
- Domec J.-C., Lachenbruch B. & Meinzer F.C. (2006) Bordered pit structure and function determine spatial patterns of air-seeding thresholds in xylem of Douglas-fir (*Pseudotsuga menziesii*; Pinaceae) trees. *American Journal of Botany* **93**, 1588–1600.
- Ellerby D.J. & Ennos A.R. (1998) Resistances to fluid flow of model xylem vessels with simple and scalariform perforation plates. *Journal of Experimental Botany* **49**, 979–985.
- Enquist B.J., West G.B. & Brown J.H. (2000) Quarter-power allometric scaling in vascular plants: functional basis and ecological consequences. In *Scaling in Biology* (eds J.H. Brown & G.B. West), pp. 167–198. Oxford University Press, Oxford, UK.
- Ewers F.W. (1985) Xylem structure and water conduction in conifer trees, dicot trees, and lianas. *International Association of Wood Anatomists Bulletin* **6**, 309–317.
- Goldstein G., Meinzer F.C. & Monasterio M. (1984) The role of capacitance in the water balance of Andean giant rosette species. *Plant, Cell & Environment* **7**, 179–186.
- Goldstein G., Andrade J.L., Meinzer F.C., Holbrook N.M., Cavelier J., Jackson P. & Silvera K. (1997) Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant, Cell & Environment* **21**, 397–406.
- Hacke U.G., Sperry J.S., Pockman W.P., Davis S.D. & McCulloh K.A. (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* **126**, 457–461.
- Hacke U.G., Sperry J.S. & Pittermann J. (2004) Analysis of circular bordered pit function II. Gymnosperm tracheids with torus-margo pit membranes. *American Journal of Botany* **91**, 386–400.
- Hacke U.G., Sperry J.S., Wheeler J.K. & Castro L. (2006) Scaling of angiosperm xylem structure with safety and efficiency. *Tree Physiology* **26**, 689–701.
- Hargrave K.R., Kolb K.J., Ewers F.W. & Davis S.D. (1994) Conduit diameter and drought-induced embolism in *Salvia mellifera* Greene (Labiatae). *New Phytologist* **126**, 695–705.
- Holbrook N.M. & Sinclair T.R. (1992) Water balance in the arborescent palm, *Sabal palmetto*. II. Transpiration and water storage. *Plant, Cell & Environment* **15**, 401–409.
- Horn H.S. (2000) Twigs, trees and the dynamics of carbon in the landscape. In *Scaling in Biology* (eds J.H. Brown & G.B. West), pp. 199–220. Oxford University Press, Oxford, UK.
- Hubbard R.M., Bond B.J. & Ryan M.G. (1999) Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiology* **19**, 165–172.
- Hubbard R.M., Stiller V., Ryan M.G. & Sperry J.S. (2001) Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. *Plant, Cell & Environment* **24**, 113–121.
- Jacobsen A.L., Ewers F.W., Pratt R.B., Paddock W.A. & Davis S.D. (2005) Do xylem fibers affect vessel cavitation resistance? *Plant Physiology* **139**, 546–556.
- Jagels R., Visscher G.E., Lucas J. & Goodell B. (2003) Paleo-adaptive properties of the xylem of *Metasequoia*: mechanical/hydraulic compromises. *Annals of Botany* **92**, 79–88.
- Jarbeau J.A., Ewers F.W. & Davis S.D. (1995) The mechanism of water-stress-induced embolism in two species of chaparral shrubs. *Plant, Cell & Environment* **18**, 189–196.
- King D.A. (1990) The adaptive significance of tree height. *The American Naturalist* **135**, 809–828.
- Koch G.W. & Fredeen A.L. (2005) Transport challenges in tall trees. In *Vascular Transport in Plants* (eds N.M. Holbrook & M.A. Zwieniecki), pp. 437–456. Academic Press, Amsterdam, the Netherlands.
- Koch G.W., Sillett S.C., Jennings G.M. & Davis S.D. (2004) The limits to tree height. *Nature* **428**, 851–854.
- Lo Gullo M.A. & Salleo S. (1992) Water storage in the wood and xylem cavitation in 1-year-old twigs of *Populus deltoides* Bartr. *Plant, Cell & Environment* **15**, 431–438.
- Loustau D., Berbigier P., Roumagnac P., Arruda-Pecheco C., David J.S., Ferreira M.I., Pereira J.S. & Tavares R. (1996) Transpiration of a 64-year-old maritime pine stand in Portugal. *Oecologia* **107**, 33–44.
- McCulloh K.A. & Sperry J.S. (2005a) The evaluation of Murray's law in *Psilotum nudum* (Psilotaceae), an analogue of ancestral vascular plants. *American Journal of Botany* **62**, 985–989.
- McCulloh K.A. & Sperry J.S. (2005b) Patterns in hydraulic architecture and their implications for transport efficiency. *Tree Physiology* **25**, 257–267.
- McCulloh K.A. & Sperry J.S. (2006) Murray's law and the vascular architecture of plants. In *Ecology and Biomechanics* (eds A.

- Herrel, T. Speck & N.P. Rowe), pp. 85–100. CRC Taylor & Francis, Boca Raton, FL, USA.
- McCulloh K.A., Sperry J.S. & Adler F.R. (2003) Do plants obey Murray's law? *Nature* **421**, 939–942.
- McCulloh K.A., Sperry J.S. & Adler F.R. (2004) Murray's law and the hydraulic vs. mechanic functioning of wood. *Functional Ecology* **18**, 931–938.
- McDowell N.G., Phillips N., Lurch C., Bond B.J. & Ryan M.G. (2002) An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. *Tree Physiology* **22**, 763–774.
- McMahon T.A. (1973) Size and shape in biology. *Science* **179**, 1201–1204.
- Meinzer F.C., Clearwater M.J. & Goldstein G. (2001) Water transport in trees: current perspectives, new insights and some controversies. *Environmental and Experimental Botany* **45**, 239–262.
- Meinzer F.C., James S.A., Goldstein G. & Woodruff D.R. (2003) Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. *Plant, Cell & Environment* **26**, 1147–1155.
- Meinzer F.C., James S.A. & Goldstein G. (2004) Dynamics of transpiration, sap flow and use of stored water in tropical forest canopy trees. *Tree Physiology* **24**, 901–909.
- Meinzer F.C., Bond B.J., Warren J.M. & Woodruff D.R. (2005) Does water transport scale universally with tree size? *Functional Ecology* **19**, 558–565.
- Meinzer F.C., Brooks J.R., Domec J.-C., Gartner B.L., Warren J.M., Woodruff D.R. & Bible K. (2006) Dynamics of water transport and storage in conifers studied with deuterium and heat tracing techniques. *Plant, Cell & Environment* **29**, 105–114.
- Meinzer, F.C., Woodruff, D.R., Domec, J.-C., Goldstein, G., Campanello, P.I., Gatti, M.G. & Villalobos-Vega, R. (2008a) Coordination of leaf and stem water transport properties in tropical forest trees. *Oecologia* (in press).
- Meinzer F.C., Bond B.L. & Karanian J.A. (2008b) Biophysical constraints on leaf expansion in a tall conifer. *Tree Physiology* **28**, 197–206.
- Mencuccini M. (2002) Hydraulic constraints in the functional scaling of trees. *Tree Physiology* **22**, 553–565.
- Mencuccini M. (2003) The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. *Plant, Cell & Environment* **26**, 163–182.
- Mencuccini M. & Magnani F. (2000) Comment on 'Hydraulic limitation of tree height: a critique,' by Becker, Meinzer and Wullschlegel. *Functional Ecology* **14**, 135–140.
- Mencuccini M., Hölttä T., Petit G. & Magnani F. (2007) Sanio's laws revisited. Size-dependent changes in xylem architecture of trees. *Ecology Letters* **10**, 1084–1093.
- Murray C.D. (1926) The physiological principle of minimum work. I. The vascular system and the cost of blood volume. *Proceedings of the National Academy of Sciences of the United States of America* **12**, 207–214.
- Nielsen E.T., Sharifi M.R., Rundel P.W., Forseth I.N. & Ehleringer J.R. (1990) Water relations of stem succulent trees in north central Baja California. *Oecologia* **82**, 299–303.
- Niklas K.J. (1994) Predicting the height of fossil plant remains: an allometric approach to an old problem. *American Journal of Botany* **81**, 1235–1242.
- Niklas K.J. & Spatz H.C. (2004) Growth and hydraulic (not mechanical) constraints govern the scaling of tree height and mass. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 15661–15663.
- Phillips N., Nagchaudhuri A., Oren R. & Katul G. (1997) Time constant for water transport in loblolly pine trees estimated from time series of evaporative demand and stem sapflow. *Trees* **11**, 412–419.
- Phillips N.G., Ryan M.G., Bond B.J., McDowell N.G., Hinckley T.M. & Čermák J. (2003) Reliance of stored water increases with tree size in three species in the Pacific Northwest. *Tree Physiology* **23**, 237–245.
- Phillips N.G., Oren R., Licata J. & Linder S. (2004) Time series diagnosis of tree hydraulic characteristics. *Tree Physiology* **24**, 879–890.
- Pittermann J. & Sperry J.S. (2003) Tracheid diameter is the key trait determining extent of freezing-induced cavitation in conifers. *Tree Physiology* **23**, 907–914.
- Pittermann J. & Sperry J.S. (2006) Analysis of freeze-thaw embolism in conifers: the interaction between cavitation pressure and tracheid size. *Plant Physiology* **140**, 374–382.
- Pittermann J., Sperry J.S., Hacke U.G., Wheeler J.K. & Sikkema E.H. (2005) Torus-margo pits help conifers compete with angiosperms. *Science* **310**, 1924.
- Pittermann J., Sperry J.S., Hacke U.G., Wheeler J.K. & Sikkema E.H. (2006a) Inter-tracheid pitting and the hydraulic efficiency of conifer wood: the role of tracheid allometry and cavitation protection. *American Journal of Botany* **93**, 1105–1113.
- Pittermann J., Sperry J.S., Wheeler J.K., Hacke U.G. & Sikkema E.H. (2006b) Mechanical reinforcement of tracheids compromises the hydraulic efficiency of conifer xylem. *Plant, Cell & Environment* **29**, 1618–1628.
- Pratt R.B., Jacobsen A.L., Ewers F.W. & Davis S.D. (2007) Relationships among xylem transport, biomechanics and storage in stems and roots of nine Rhamnaceae species of the California chaparral. *New Phytologist* **174**, 787–798.
- Ryan M.G. & Yoder B.J. (1997) Hydraulic limits to tree height and tree growth: what keeps trees from growing beyond a certain height? *Bioscience* **47**, 235–242.
- Ryan M.G., Phillips N. & Bond B.J. (2006) The hydraulic limitation hypothesis revisited. *Plant, Cell & Environment* **29**, 367–381.
- Scholz F.G., Bucci S.J., Goldstein G., Meinzer F.C., Franco A.C. & Miralles-Wilhelm F. (2007) Biophysical properties and functional significance of stem water storage tissues in neotropical savanna trees. *Plant, Cell & Environment* **30**, 236–248.
- Schulte P.J. & Castle A.L. (1993) Water flow through vessel perforation plates – the effects of plate angle and thickness for *Liriodendron tulipifera*. *Journal of Experimental Botany* **44**, 1143–1148.
- Siau J.F. (1971) *Flow in Wood*. Syracuse University Press, Syracuse, NY, USA.
- Simpson W.T. (1993) Specific gravity, moisture content and density relationship for wood. Gen. Tech. Rep. FPL-GTR-76. Madison, WI: US Department of Agriculture, Forest Service, Forest Products Laboratory 13.
- Sperry J.S. & Saliendra N.Z. (1994) Intra- and inter-plant variation in xylem cavitation in *Betula occidentalis*. *Plant, Cell & Environment* **17**, 1233–1241.
- Sperry J.S., Hacke U.G. & Pittermann J. (2006) Size and function in conifer tracheids and angiosperm vessels. *American Journal of Botany* **93**, 1490–1500.
- Stratton L., Goldstein G. & Meinzer F.C. (2000) Stem water storage capacity and efficiency of water transport: their functional significance in a Hawaiian dry forest. *Plant, Cell & Environment* **23**, 99–106.
- Taneda H. & Tateno M. (2004) The criteria for biomass partitioning of the current shoot: water transport versus mechanical support. *American Journal of Botany* **91**, 1949–1959.
- Waring R.H. & Running S.W. (1978) Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas-fir. *Plant, Cell & Environment* **1**, 131–140.
- Waring R.H., Whitehead D. & Jarvis P.G. (1979) The contribution

- of stored water to transpiration in Scots pine. *Plant, Cell & Environment* **2**, 309–317.
- Weitz J.S., Ogle K. & Horn H.S. (2006) Ontogenetically stable hydraulic design in woody plants. *Functional Ecology* **20**, 191–199.
- West G.B., Brown J.H. & Enquist B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122–126.
- Wheeler J.K., Sperry J.S., Hacke U.G. & Hoang N. (2005) Inter-vessel pitting and cavitation in woody Rosaceae and other vesselled plants: a basis for a safety vs. efficiency trade-off in xylem transport. *Plant, Cell & Environment* **28**, 800–812.
- Williams M., Rastetter E.B., Fernandes D.N., Goulden M.L., Wofsy S.C., Shaver G.R., Melillo J.M., Munger J.W., Fan S.-M. & Nadelhoffer K.J. (1996) Modelling the soil-plant-atmosphere continuum in a *Quercus-Acer* stand at Harvard forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. *Plant, Cell & Environment* **19**, 911–927.
- Woodruff D.R., Bond B.J. & Meinzer F.C. (2004) Does turgor limit growth in tall trees? *Plant, Cell & Environment* **27**, 229–236.
- Woodruff D.R., McCulloh K.A., Warren J.M., Meinzer F.C. & Lachenbruch B. (2007) Impacts of tree height on leaf hydraulic architecture and stomatal control in Douglas-fir. *Plant, Cell & Environment* **30**, 559–569.
- Zaehle S. (2005) Effect of tree height on tree hydraulic conductance incompletely compensated by xylem tapering. *Functional Ecology* **19**, 359–364.
- Zimmermann M.H. (1978) Hydraulic architecture of some diffuse porous trees. *Canadian Journal of Botany* **56**, 2286–2295.
- Zimmermann M.H. (1983) *Xylem Structure and the Ascent of Sap*. Springer-Verlag, Berlin, Germany.
- Zwieniecki M.A., Melcher P.J. & Holbrook N.M. (2001) Hydraulic properties of individual xylem vessels of *Fraxinus americana*. *Journal of Experimental Botany* **52**, 257–264.

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APPENDIX

Calculation of network conductivities (Figs 2 & 3)

The calculation assumes an arbitrary branching network of a given branching pattern and length. In Fig. 2, we assumed a trunk (rank $i = 0$) dividing into two daughter branches (rank $i = 1$), each of which divides into two granddaughter branches (rank $i = 2$). The equations can be modified for any pattern or number of ranks, but with no effect on the relative pattern of network conductivities. There is an arbitrary, but fixed, volume of vascular tissue with which to pipe the network. Because all the branch lengths are constant, a fixed volume translates into a fixed cross-sectional area summed across all ranks (A). The conductance (volume flow rate per pressure difference) of the network is solved as a function of how this area is distributed across the ranks (A_i) and the number of pipes per rank (N_i). Because the lengths are fixed, the network conductance is proportional to the conductivity (volume flow rate per pressure gradient) of each rank in series. It is simpler to express this series conductivity as the reciprocal series resistivity (R) because the rank resistivities are additive. Assuming the Hagen–Poiseuille equation:

$$R = [128\eta k/\pi](N_0^{-1}D_0^{-4} + N_1^{-1}D_1^{-4} + N_2^{-1}D_2^{-4}), \quad (\text{A1})$$

where η is the viscosity, D_i is the pipe diameter and N_i is the pipe number of rank i , and k is the factor by which the resistivity of the xylem conduit exceeds the theoretical Hagen–Poiseuille value (greater than 1 because of end-wall effects). The number of conduits in the terminal rank (N_2) is arbitrarily chosen. If the number ratio N_{i+1}/N_i is assumed constant (N_R),

$$N_1 = N_2 N_R^{-1} \quad \text{and} \quad N_0 = N_2 N_R^{-2}. \quad (\text{A2})$$

If the diameter ratio D_{i+1}/D_i is assumed constant (D_R), the ratio of the distal to proximal cross-sectional areas of the conduits (A_R) is

$$A_R = D_R^2 N_R. \quad (\text{A3})$$

The total cross-sectional area of the terminal rank (A_2) can be solved as

$$A_2 = A A_R^2 / (1 + A_R + A_R^2), \quad (\text{A4})$$

which in terms of D_R and N_R is

$$A_2 = A (N_R^{-2} D_R^{-4} + N_R^{-1} D_R^{-2} + 1)^{-1}. \quad (\text{A4a})$$

The diameter of the terminal conduits (D_2) can be solved by substituting Eqn A4 for A_2 into the following:

$$D_2 = [4A_2 / (\pi N_2)]^{0.5} \quad (\text{A5})$$

and the other diameters solved as

$$D_1 = D_2 D_R^{-1} \quad \text{and} \quad D_0 = D_2 D_R^{-2}. \quad (\text{A5a})$$

Substituting Eqns 2 and 5 into Eqn 1 gives the series resistivity as

$$R = [128\eta k/\pi](N_2/A_2^2)(N_R^2 D_R^8 + N_R D_R^4 + 1). \quad (\text{A6})$$

Substituting Eqn A4a into Eqn A6 gives R as a function of A , N_2 , D_R and N_R . By holding A and N_2 constant, the effect of different D_R and N_R combinations on R can be computed as in Fig. 2. The conductivity contour lines in Fig. 2 were computed by solving for N_R as a function of D_R and R using the Newton–Raphson method. The shape of the contour map does not depend on the arbitrary choices for A , N_2 or the branching architecture (number of ranks or mother-to-daughter branch ratio). These calculations are the same as that used previously, except that we express the network conductivity as a function of N_R and D_R instead of the conductivity ratio ($K_R = N_R D_R^4$; McCulloh & Sperry 2005b).

If the cross-sectional area of wood is assumed constant from trunk to twig, the relationship between the conduit frequency (f) and the average diameter (Fig. 1a) yields the corresponding relationship between N_R and D_R :

$$f \propto D^c, N_R = D_R^c, \quad (\text{A7})$$

where 'c' is the slope of the log–log relation between f and D (Fig. 1a). Equation A7 gives the dotted conifer ($c = -1.59$) and angiosperm ($c = -2.25$) trajectories in Fig. 2. The corresponding network conductivities for conifers and angiosperms in Fig. 3 (upper volume = conduit curves) were computed from Eqn A6 from the corresponding N_R versus D_R relationships, and inverting the resistivities to give the conductivities. The 'k' term was held constant across both wood types.

To compute the network conductivity on the basis of fixed wood volume rather than fixed conduit volume, the arbitrary cross-sectional area, A , is designated as a wood area rather than a conduit area. The ratio of conduit-to-wood area (also volume), F , adjusts Eqn A4a to give the cumulative conduit area of the terminal unit (A_2):

$$A_2 = AF(N_R^{-2}D_R^{-4} + N_R^{-1}D_R^{-2} + 1)^{-1}. \quad (\text{A8})$$

The resistivity for a given A , D_R and N_R becomes proportional to (from Eqn A6)

$$R \propto N_2 / F^2. \quad (\text{A9})$$

In terms of conductivity, Eqn A9 shows that reducing F from 1 to 0.41 for conifers causes an 83% reduction in conductivity (shown in Fig. 3, conifer line for volume = wood), and reducing F from 1 to 0.08 for angiosperms causes a 99.4% reduction (not shown). Relaxing the constraint on the number of terminal conduits (N_2) allows it to be reduced in angiosperms relative to conifers, as indicated from the different frequency versus diameter relationships. Lower N_2 means a greater diameter range (Eqn A5 & A5a) and lower resistivity (Eqn A9). Decreasing N_2 by a factor of 20–30 in angiosperms compensates for their lower F , equalizing the network resistivity of the two wood types (Fig. 3, angiosperm conductivities for volume = wood curves, range indicated by dotted curves).

Height analysis (Fig. 4)

From the Hagen–Poiseuille equation, conductance (K) is related to conduit diameter (d):

$$K \propto Afd^4 / H, \quad (\text{A10})$$

where f is the conduit frequency, A is the xylem cross-sectional area and H is the stem length. The proportionality is approximate for a distribution of conduits with a mean d . If d and f are constant with height (no taper),

$$K \propto AH^{-1}. \quad (\text{A11})$$

Assuming area-preserving branching, xylem volume (V) is proportional to

$$V \propto AH. \quad (\text{A12})$$

These proportionalities are plotted for $A \propto H^3$ in Fig. 4a (lower conductance curve, volume curve), which assumes that the basal diameter is proportional to $H^{1.5}$ (McMahon 1973), and that the conducting xylem area is proportional to the basal area.

The observed increase in conduit diameter (d) and decrease in frequency (f) moving from twig to trunk (Fig. 1a) has the advantage of minimizing the dependence of conductance on height in Eqn A10. We calculate that the maximum effect of the taper is to increase the H exponent in Eqn A11 from -1 to -0.35 . This makes $K \propto H^{2.65}$ with taper (Fig. 4a, upper conductance curve) versus $K \propto H^2$ without taper (lower curve) when we assume that $A \propto H^3$, as in the Fig. 4 example. The effect of the taper was calculated for a straight column representing all of the tree's branches fused together. The column 'grew' in fixed height increments, representing the collective terminal extension growth. The extension growth had a cross-sectional area required for diameter to be proportional to $H^{1.5}$. Each increment in H thus came with an increased girth, which was laid down across the proximal stem, representing growth rings. The conduit diameter of the terminal extension 'growth' was constant, but the conduit diameters of the radial 'growth ring' were increased by a fixed ratio moving down to the trunk across previous extension increments (proximal/distal diameter ratio = 0.9). The conduit frequency (f) was given by the angiosperm relationship with the diameter in Fig. 1a. The maximum vessel diameter was capped at 20 times the terminal diameter to reflect the maximum range of vessel diameters in Fig. 1a and to represent a constraint on the maximum vessel diameter. Further increases in the rate of the diameter taper had negligible effects on the conductance by height proportionality. Substituting the conifer diameter versus frequency trend in Fig. 1a also had only a minor effect.