

Moving water well: comparing hydraulic efficiency in twigs and trunks of coniferous, ring-porous, and diffuse-porous saplings from temperate and tropical forests

Katherine McCulloh¹, John S. Sperry², Barbara Lachenbruch¹, Frederick C. Meinzer³, Peter B. Reich⁴ and Steven Voelker¹

¹Department of Wood Science and Engineering, Oregon State University, Corvallis, OR 97330, USA; ²Department of Biology, University of Utah, Salt Lake City, UT 84112, USA; ³USDA Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331, USA; ⁴Department of Forest Resources, University of Minnesota, St Paul, MN 55108, USA

Summary

Author for correspondence:

Katherine McCulloh

Tel: +1 541 737 4208

Email: kate.mcculloh@oregonstate.edu

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- Coniferous, diffuse-porous and ring-porous trees vary in their xylem anatomy, but the functional consequences of these differences are not well understood from the scale of the conduit to the individual.
- Hydraulic and anatomical measurements were made on branches and trunks from 16 species from temperate and tropical areas, representing all three wood types. Scaling of stem conductivity (K_h) with stem diameter was used to model the hydraulic conductance of the stem network.
- Ring-porous trees showed the steepest increase in K_h with stem size. Temperate diffuse-porous trees were at the opposite extreme, and conifers and tropical diffuse-porous species were intermediate. Scaling of K_h was influenced by differences in the allometry of conduit diameter (taper) and packing (number per wood area) with stem size.
- The K_h trends were mirrored by the modeled stem-network conductances. Ring-porous species had the greatest network conductance and this value increased isometrically with trunk basal area, indicating that conductance per unit sapwood was independent of tree size. Conductances were lowest and most size-dependent in conifers. The results indicate that differences in conduit taper and packing between functional types propagate to the network level and have an important influence on metabolic scaling concepts.

Introduction

Plant carbon gain and survival are intimately coordinated with the properties of the hydraulic networks supplying water to leaves. Given that the xylem fulfills such a fundamental demand, the large amount of structural diversity in hydraulic architecture among different species may be somewhat surprising. Among seed plants, there are three radically different wood types – coniferous, diffuse-porous and ring-porous. Understanding the functional consequences associated with each of these wood types will lead to a more fundamental appreciation of how all three manage to coexist at the global scale, as well as what drives observed patterns of presence or absence of each group at

smaller landscape scales. Our goal in this study was to compare the hydraulic architecture of species from these three wood types during the same life stage to evaluate broad patterns of xylem form and function, including differences in the allometry of conduit diameter (taper) and conduit packing (number per wood area) with stem size. These measures enabled us to compare the hydraulic efficiency of these groups at integrated scales, ranging from a single conduit to a whole stem network, and to compare results with existing theory. Hydraulic efficiency, depending on the measurement scale, is defined as the hydraulic conductivity or conductance per unit investment in transport, where investment can be quantified as cross-sectional area of conduit, tissue, branch or trunk.

The three wood types vary in the complexity of cell types and patterns of conduit distribution (vessels or tracheids). Conifer wood is relatively simple, with its tracheids functioning in both water transport and structural support to the plant form. Angiosperm wood is more complex, and the tasks of transport and support are primarily performed by vessels and fibers, respectively. Within angiosperms, vessels of diffuse-porous wood show little variation in diameter in the radial direction at a given point in the vascular network (Panshin & de Zeeuw, 1970). Ring-porous wood contains growth rings with wide vessels produced at the beginning of each growing season, followed by fibers and a few narrow vessels, and the sapwood is often composed of only the outermost annual ring (Panshin & de Zeeuw, 1970). The wood types also vary in their geographic distribution. Species with truly ring-porous wood are largely restricted to north temperate habitats (Gilbert, 1940; Wheeler *et al.*, 2007), whereas diffuse-porous species span a broad spectrum of latitudes in both hemispheres. Conifers are predominantly restricted to higher latitudes, but also exist in the tropics and subtropics, especially in the southern hemisphere.

Although conifer wood is simpler than angiosperm wood, it is not necessarily less efficient. At the conduit and sapwood scale, single-celled tracheids have been shown to be as efficient as multicelled vessels of the same diameter (Pittermann *et al.*, 2005). This similar conductivity per investment is the result of more conductive pits between conifer tracheids than between vessels, which compensates for the resistance caused by the shorter length of the tracheid. Although tracheids can match the efficiency of vessels of the

same diameter, vessels are able to achieve greater maximum diameters than tracheids, with a concomitant increase in efficiency (Sperry *et al.*, 2006, 2008).

At the network scale, the degree to which conduits narrow and multiply, moving from trunk to twig, can have a major influence on whole-shoot conductance (Sperry *et al.*, 2008). When taper is sufficient to eliminate the effect of increasing path length (Enquist *et al.*, 2000), whole-tree conductance will scale isometrically with basal area (or, equivalently, with trunk diameter to the second power; Mencuccini, 2002). The effect of taper is modulated by the fact that as conduits become narrower, there are more of them conducting in parallel (Sperry *et al.*, 2008).

Here, we consider vascular traits at the conduit, tissue, stem, and network levels in conifers, diffuse-, and ring-porous angiosperms. We evaluate how various measures of efficiency scale from conduits to entire vascular networks in these widely contrasting wood types.

Materials and Methods

Species and plant collection

Saplings from three to eight species per wood type were collected from naturally occurring stands. Species were selected that were locally abundant, native, and, with the exception of two *Acer* species, representatives from different genera. Saplings were chosen that were 1–4 m tall (Table 1), with narrow enough trunks to fit the tubing available for hydraulic measurements. Within each wood type, some species were found in clearings, while others were in the under-

Table 1 Mean architectural characteristics for the sampled saplings, by species

Species	Habitat and wood type	Height (m)	Leaf area (m ²)	Trunk diameter (mm)	Branch diameter (mm)	Trunk sample size	Branch sample size
<i>Anacardium excelsum</i>	Trop DP	1.8 (0.5) ^a	0.9 (0.5)	14.3 (2.6)	7.1 (1.5)	4	17
<i>Cordia alliodora</i>	Trop DP	1.4 (0.9)	0.5 (0.7)	21.1 (7.2)	3.2 (0.7)	4	19
<i>Ficus insipida</i>	Trop DP	3.6 (0.9)	1.5 (0.5)	25.1 (0.2)	9.7 (1.1)	4	19
<i>Luehea seemannii</i>	Trop DP	2.6 (1.0)	0.6 (0.3)	18.4 (5.0)	5.3 (1.2)	4	18
<i>Acer circinatum</i>	Tem DP	1.5 (0.2)	0.2 (0.1)	9.4 (2.5)	1.6 (0.3)	8	20
<i>Acer macrophyllum</i>	Tem DP	2.8 (0.3)	0.5 (0.2)	12.7 (1.5)	3.2 (0.3)	8	20
<i>Alnus rubra</i>	Tem DP	1.9 (0.3)	0.9 (0.6)	10.9 (2.1)	1.8 (0.3)	8	20
<i>Arbutus menziesii</i>	Tem DP	1.3 (0.1)	0.2 (0.0)	12.9 (1.2)	3.4 (0.7)	8	20
<i>Fraxinus nigra</i>	Tem RP	2.5 (1.0)	0.8 (0.5)	14.7 (1.0)	6.1 (0.5)	8	20
<i>Quercus ellipsoidalis</i>	Tem RP	1.0 (0.2)	0.4 (0.2)	10.6 (2.2)	2.5 (0.2)	8	21
<i>Robinia pseudoacacia</i>	Tem RP	1.6 (0.7)	1.5 (1.0)	13.2 (4.5)	3.5 (0.9)	6	15
<i>Abies grandis</i>	Tem CON	1.3 (0.3)	0.6 (0.5)	17.3 (5.0)	3.2 (0.2)	4	20
<i>Pinus ponderosa</i>	Tem CON	0.6 (0.0)	0.2 (0.0)	12.1 (1.9)	3.1 (0.3)	7	20
<i>Pseudotsuga menziesii</i>	Tem CON	1.5 (0.2)	1.8 (0.8)	22.8 (4.9)	4.6 (0.7)	4	20
<i>Thuja plicata</i>	Tem CON	1.6 (0.1)	1.0 (0.2)	18.3 (2.0)	3.3 (0.6)	4	20
<i>Tsuga heterophylla</i>	Tem CON	1.9 (0.4)	3.2 (1.6)	20.3 (1.4)	3.8 (0.2)	4	20

Trop, tropical; Tem, temperate; DP, diffuse-porous; RP, ring-porous; CON, conifers.

^aMeans are the grand means between $n = 4$ individuals. Standard deviations are shown in parentheses.

story. All individuals of a species were collected from the same light environment, but within each wood type we sampled some species that thrive in sun and others that thrive in shade. Our goal was not to compare sun vs shade, but rather to identify patterns within and among wood types that dominate regardless of light regime.

Four individuals from each species were cut near the base of the stem and immediately transferred to a container of 0.5% filtered aqueous acid fuchsin, and the length of the stem remaining from the cut to the ground was recorded. The dye taken up by the trunk allowed conductive and non-conductive regions of the stem to be distinguished. The saplings were then sealed in double plastic bags and taken to the laboratory for measurements.

Saplings of four diffuse-porous species were collected in the Republic of Panama in March 2005. Saplings of *Anacardium excelsum* (Bentner & Balb. Ex Kunth) Skeels, *Cordia alliodora* (R. & P.) Oken., *Ficus insipida* Willd., and *Luehea seemannii* Triana & Planch were collected at Parque Metropolitano, Parque Nacional Soberanía, and in the laboratory clearing on Barro Colorado Island (BCI, 9°N 79°W). All laboratory measurements were made in the Smithsonian Tropical Research Institute facilities on BCI.

The five species of conifers and four more species with diffuse-porous wood were harvested in the summers of 2006 and 2007, respectively. All species were collected in and around Corvallis, Oregon USA (45°N 123°W), except *Pinus ponderosa* Laws, which was collected near Metolius, Oregon. The additional coniferous representatives were *Abies grandis* (Dougl.) Lindl., *Pseudotsuga menziesii* (Mirb.) Franco., *Tsuga heterophylla* (Rafn.) Sarg., and *Thuja plicata* D. Don. The temperate diffuse-porous species were *Alnus rubra* Bong., *Acer macrophyllum* Pursh, *Acer circinatum* Pursh, and *Arbutus menziesii* Pursh. The laboratory measurements for these species were completed on the campus of Oregon State University (OSU).

Representatives from three species of ring-porous trees were collected in the Cedar Creek Ecosystem Science Reserve (45°N, 93°W) in central Minnesota, USA, during summer 2008. Individuals of *Fraxinus nigra* Marsh., *Quercus ellipsoidalis* E. J. Hill, and *Robinia pseudoacacia* L. were harvested, the leaves removed, and branch samples were shipped overnight to OSU for analysis. A delay in shipping in two of the *Robinia* individuals and one *Quercus* made the samples unsuitable for use. To replace the lost *Robinia* samples, two invasively growing *Robinia* individuals were cut in Corvallis, Oregon.

Hydraulic measurements

In the laboratory on BCI and at OSU, hydraulic conductivity (K_h) was measured for both the terminal branches and trunk of all individuals. Terminal branches (referred to simply as 'branches' hereafter) were defined as the distal

unbranched extremities of the stem network. For hydraulic studies, we selected three to seven leaf-bearing branches from each sapling that represented the range of that sapling's terminal branch diameters. We chose fewer than five branch samples only on individuals where more were not available. One segment (4–11 cm long, depending on what was available) was cut under water between the branch's base and its most proximal leaf. In addition, one to two trunk segments *c.* 10 cm long were excised. The lower trunk segment came from the portion that was originally *c.* 10 cm above ground, and *c.* 5–10 cm was left between the two segments.

The ends of all segments (branch and trunk) were trimmed with a sharp razor blade before measuring. We then applied a quick-drying superglue that functions on wet materials (Loctite, Henkel Group, Avon, OH, USA) to the area of the basal end of the trunk segments that were not stained by the acid fuchsin. The glue prevented flow through this nonfunctional region from being included in the K_h measurement. All segments were flushed to measure the maximum hydraulic conductivity.

In Panama, segments were flushed using a pressure chamber (PMS Instrument Co., Corvallis, OR, USA). One end of the segment was attached to solution-filled tubing that was inserted through the chamber lid and submerged into a vial of solution within the chamber. The perfusing solution was filtered and deionized water was acidified to pH 2 with HCl. The pressure in the chamber was raised to 0.2 MPa and the stem was flushed for either 20 min or, for segments with high porosity, until at least two full vials of the solution (*c.* 200 ml) had been pushed through the stem.

Branches of *Luehea* contained much mucilage, which impeded the measurements of hydraulic conductivity. In an attempt to remove the mucilage, the stem segments were submerged in water in a vial on a stir plate and the water was agitated overnight. As a further attempt to remove the mucilage, we perfused the stems with the pH 2 HCl solution. To keep all measurements consistent, the pH 2 solution was used for measurements on stems for all species. However, in spite of our efforts, the measured K_h values from *Luehea* were approximately two orders of magnitude below all other measurements on other species and were not considered reliable, so the hydraulic data were not used.

In Oregon, the branch and trunk segments were also flushed with filtered, distilled pH 2 water before hydraulic measurements. Embolisms were removed by submerging the stem segments in the solution in a vacuum chamber overnight. While this process infiltrates nonxylary airspaces with water, the proportion that these spaces would add to the conductivity should be insignificant because of their small dimensions.

To measure hydraulic conductivity, a hydrostatic pressure head was used to induce flow through the segments. The resulting volume flow rate was measured by timing the

intervals for water to reach successive gradations on a pipette attached with tubing to the distal end of the segment. If flow was observed with no pressure head, this volume flow rate was measured and subtracted from the flow induced with the hydrostatic pressure. K_h was calculated by dividing the mass flow rate of water (Q) flowing through the stem by the hydrostatic pressure gradient (ΔP per stem length) along the stem (reported here in units of $\text{kg m MPa}^{-1} \text{s}^{-1}$). The area-specific (K_S) and leaf area-specific (K_L) conductivities were determined from K_h divided by the cross-sectional area of the stem or the leaf area supplied by that stem segment, respectively.

Xylem anatomical measurements

The xylem conduits (vessels or tracheids) were analyzed on all samples on which hydraulic measurements were made. To make these measurements, cross-sections of each branch or trunk segment were made using either a sharp razor blade or a sliding microtome. Sections were mounted in glycerin and imaged using a digital camera mounted on a Nikon Eclipse E400 compound microscope. The image-analysis program ImageJ (National Institutes of Health, Bethesda, MD, USA; <http://rsb.info.nih.gov/ij/>) was used to measure the lumen area of all conduits in three to four wedge-shaped sections from the bark to pith, and at least 100 conduits were measured from each branch or trunk segment. For angiosperms, lumen cross-sectional areas were then converted to diameters by assuming the conduits were circular. For conifers, lumen cross-sectional areas were converted to diameters by assuming the tracheids were square, using $d = A^{1/2}$, where A is the lumen area. Areas of the wedges in which the conduits were measured were determined to calculate the number of conduits per area (conduit frequency), and to scale the number of conduits to the stem cross-sectional area.

The mean conduit hydraulic diameter for each branch and trunk sample was calculated as $d_h = (\sum d^4/n)^{1/4}$, where d is the diameter of each conduit and n is the number of conduits measured in the sample. This value is the diameter of a conduit with the average Hagen–Poiseuille (HP) lumen conductivity. The HP equation was then used to calculate the theoretical hydraulic conductivity for a given conduit diameter ($K_h = (\pi r^4)/(8\mu)$), where r is the conduit radius, and μ is the dynamic viscosity. For plotting diameter vs the number of conduits per wood area (the packing function), we used the diameter corresponding to the average lumen cross-sectional area. This area-weighted mean conduit diameter (d_A) was calculated for each segment as $d_A = (\sum d^2/n)^{1/2}$.

Leaf area measurements

The leaf areas of all saplings were determined to relate to the saplings' hydraulic and anatomical properties. We esti-

mated total leaf area for each sapling, as well as for each branch segment on which hydraulic measurements were made. In Panama, a leaf area meter (Li-3100C; Li-Cor Biosciences, Lincoln, NE, USA) was used. In Minnesota, leaves were scanned with a flatbed scanner and the images analyzed using ImageJ. In Oregon, both a leaf area meter and flatbed scanner were used.

For angiosperms, all leaves were measured, but we subsampled for the conifers. All conifer needles were dried in a drying oven for 3 d at 60°C and weighed. For a subset of the needles from each species, the leaf area was measured on images from a flatbed scanner and then the needles were dried and weighed. This subset was used to calculate a species-specific leaf area per mass relationship, which was used to scale the samples of needle masses to leaf areas. For the conifers, the one-sided leaf areas were doubled to account for the more vertical positioning of the needles.

Calculation of stem network conductances

Empirical relationships between hydraulic conductivity and stem diameter for each functional group were used to calculate the hydraulic conductance ($\text{kg MPa}^{-1} \text{s}^{-1}$) of a tree-sized stem network. The stem network was identical to the self-similar one modeled by West *et al.* (1999) (WBE). We chose this model for two reasons: (1) to enable comparison of our empirically based conductance scaling with WBE theory, and (2) to have a simple, idealized model of branching structure that we could hold constant across all groups to isolate the effects of differing branch vascular properties on network conductances.

For all groups the branching ratio (daughter : mother branches) was held constant at 2, and the terminal branch size was held constant with a basal diameter of 0.005 m and a length of 0.15 m. Proximal branch diameter was increased by a factor of 1.41 across adjacent branch ranks to maintain area-preserving branching. Proximal branch length was increased by a factor of 1.26 ($= 2^{0.33}$), which results in the network converging on elastic similarity with size (Enquist *et al.*, 2000). The foregoing rules result in branch length and diameter being constant for all branches of a given rank. We computed conductances for networks ranging from 2 to 20 branching ranks, which corresponded to a range of trunk diameters. To compute network conductances, we took the branch diameter of each rank and assigned a K_h value from the empirical K_h -vs-stem diameter regressions. The stem K_h was converted to conductance (k) by dividing by branch length. Conductance of each rank in parallel was the sum of all branch conductances in the rank. The network conductance was calculated as the series conductance of all branch ranks ($=$ the sum of rank resistances). To compare network conductances between wood types, all aspects of the stem network were held constant, with only

the K_h values differing according to the K_h -by-stem diameter regressions.

Statistical analyses

All analyses comparing physiological and anatomical characteristics were made using the standard major axis (SMA) line-fitting method. The scaling coefficients and parameters were calculated using SMATR freeware (Warton *et al.*, 2006; <http://www.bio.mq.edu.au/ecology/SMATR/>). This software was also used to determine the cases in which slope values from intraspecific comparisons differed from one another. For the model analysis, ordinary least-squares regressions (OLS) were used to calculate expected stem hydraulic conductivity from stem diameter. OLS is more appropriate for predicting one variable from another than SMA analyses (Sokal & Rohlf, 1995). An ANOVA with a type III sum of squares, group, individual and organ (meaning branch or trunk) as factors, and species nested within group was performed to test for differences among xylem types and organ types in conduit diameter, conduit frequency and the proximity to the absolute maximum conduit packing line (i.e. $\log(\text{conduit frequency})/\log(\text{conduit diameter})$). As a further test to ensure we could use all segments as data points, we conducted SMA analyses using SMATR to test for differences between SMA slopes for species within each group.

Results

Our initial goal was to examine hydraulic efficiency in the three main wood types, but our results suggested that temperate vs tropical diffuse-porous species segregated into two largely nonoverlapping groups (Fig. 1), differing in mean vessel diameter (t -test P -value < 0.0001). These two groups were therefore treated separately for subsequent analyses. For all four groups, each segment was used as a data point because the ANOVA testing the variation at the different levels (i.e. group, species, organ) indicated that group was indeed the most important factor in the conduit diameter, conduit frequency and the proximity to the packing line comparisons (type III sum of squares: group = 310.1, species = 0.2, organ = 18.2; Supporting Information, Table S1). The SMA analyses comparing slopes from each species within a group also showed minimal differences (one ring-porous species had a marginally different slope than one other species ($P = 0.03$); Table S2). Both of these results justified the use of each branch and trunk segment as an individual data point.

In each group, the conduit diameters and frequencies (conduits per area) showed a typical inverse relationship, which we refer to as the 'packing function' (Fig. 1): the larger the conduit diameter, the fewer conduits that can occupy a given space in the wood. The 'packing limit'

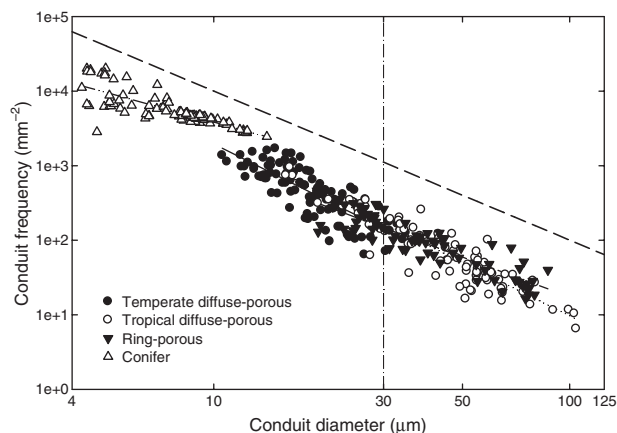


Fig. 1 The area-weighted conduit diameter vs conduit frequency relationship. Symbols indicate individual twigs or trunks from different wood type or habitats. Standard major axis (SMA) analyses ($P < 0.001$) are shown for each group: temperate diffuse-porous (solid); tropical diffuse-porous (dotted); ring-porous (dashed); conifers (dash-dot-dotted). The long-dashed line is the geometric packing limit of the maximum number of conduits of a given diameter per mm^2 , assuming square packing. The square-packing limit was calculated as $1/d^2$. The dash-dotted line corresponds to 30- μm -diameter conduits (see text for details).

(Fig. 1, dashed line) with a log–log slope of -2 represents the greatest possible number of conduit lumens that can be packed per unit area, assuming square packing.

Conduit diameter and frequency and the resulting packing functions differed between groups (Fig. 1, Table 2, Table S1). The conifer species had the narrowest conduit diameters and the most conduits per mm^2 at both the trunk and branch ranks. The slope of the conifer packing function (-1.6 , $r^2 = 0.66$; Table 3 contains scaling coefficients for Figs 1–5) was shallower than -2 ($P < 0.0001$), indicating that the lumens occupied a lower fraction of the wood area in the twigs (where the lumens are narrow) than in the trunks. Conifers, with lumens occupying from 28 to 37% of the total wood area were closer to the packing limit than were angiosperms. The ring-porous and tropical diffuse-porous species had the widest diameter conduits and the fewest conduits per mm^2 . The ring porous SMA slope was not different from -2 ($P = 0.65$), and lumens occupied an average of 9% of the total wood area. The diffuse-porous slopes were steeper than -2 (tropical = -2.6 , $r^2 = 0.85$; temperate = -2.9 , $r^2 = 0.66$, F -test indicating difference from -2 , $P < 0.001$ for both groups), indicating a greater fraction of lumen area in their average twig (tropical = 20%, temperate = 16%) than in their average trunk (tropical = 7%, temperate = 10%).

Wood traits scaled with stem sizes examined here in all groups (Fig. 2). Conduit diameter increased with stem diameter, indicating significant taper in conduit size moving from trunks to twigs (Fig. 2a). However, there were large differences between groups in both the degree of conduit

Table 2 Mean xylem characteristics for the species of saplings

Species	Conduit diameter (μm)		Conduit frequency (mm^2)		Hydraulic diameter (μm)	
	Trunk	Branch	Trunk	Branch	Trunk	Branch
Tropical diffuse-porous						
<i>Anacardium excelsum</i>	53.0 (6.4) ^a	47.0 (5.7)	23.1 (7.4)	54.7 (15.5)	61.3 (9.5)	54.7 (6.8)
<i>Cordia alliodora</i>	38.7 (10.6)	27.6 (8.4)	50.6 (27.3)	287 (208)	41.6 (10.7)	30.6 (8.6)
<i>Ficus insipida</i>	96.3 (7.8)	58.0 (8.1)	10.0 (2.4)	51.0 (22.8)	105.1 (6.3)	64.2 (9.3)
<i>Luehea seemannii</i>	51.2 (15.8)	33.4 (8.1)	20.6 (8.5)	170 (60.4)	54.6 (20.2)	35.8 (11.1)
Mean	59.8 (25.1)	41.5 (13.7)	26.1 (17.3)	140 (112)	65.6 (27.6)	46.3 (15.8)
Temperate diffuse-porous						
<i>Acer circinatum</i>	18.6 (2.3)	10.4 (1.9)	136 (29.0)	833 (232)	25.0 (0.2)	14.3 (2.0)
<i>Acer macrophyllum</i>	24.7 (2.4)	16.1 (2.6)	113 (37.7)	395 (118)	30.7 (2.9)	21.9 (2.9)
<i>Alnus rubra</i>	25.3 (5.0)	14.9 (2.0)	184 (72.0)	585 (157)	30.9 (1.9)	19.9 (2.6)
<i>Arbutus menziesii</i>	18.8 (3.9)	11.8 (1.1)	218 (103)	1019 (189)	22.6 (1.6)	16.7 (1.4)
Mean	21.9 (3.6)	13.3 (2.6)	198 (109)	708 (274)	27.3 (4.2)	18.2 (3.4)
Ring-porous						
<i>Fraxinus nigra</i>	67.4 (6.0)	32.8 (2.9)	31.0 (11.7)	101 (16.3)	88.0 (3.8)	42.5 (5.4)
<i>Quercus ellipsoidalis</i>	51.2 (9.1)	23.8 (1.5)	57.9 (36.5)	227 (73.8)	66.5 (9.2)	28.9 (2.4)
<i>Robinia pseudoacacia</i>	61.4 (6.9)	31.7 (6.2)	29.4 (10.3)	133 (58.8)	85.0 (11.8)	40.2 (7.0)
Mean	60.0 (8.2)	41.5 (13.7)	26.1 (17.3)	141 (112)	79.8 (11.6)	37.2 (7.3)
Conifer						
<i>Abies grandis</i>	6.4 (0.7)	5.6 (1.4)	7401 (1436)	12098 (6474)	10.3 (3.6)	8.0 (2.4)
<i>Pinus ponderosa</i>	6.5 (1.0)	5.6 (1.1)	4906 (479)	6908 (1018)	9.1 (1.0)	7.0 (1.2)
<i>Pseudotsuga menziesii</i>	11.9 (2.1)	8.8 (0.9)	2939 (579)	4369 (275)	15.9 (3.0)	11.6 (1.0)
<i>Thuja plicata</i>	11.9 (0.5)	9.2 (0.7)	2970 (133)	4487 (300)	15.6 (0.8)	11.7 (1.3)
<i>Tsuga heterophylla</i>	11.6 (0.8)	8.6 (0.4)	3180 (448)	4811 (386)	14.7 (0.9)	10.7 (0.4)
Mean	9.7 (2.9)	7.6 (1.8)	4280 (1927)	6535 (3277)	13.1 (3.2)	9.8 (2.2)

^aSpecies trunk and branch means are the grand mean of the average values from three to four individuals. Standard deviations are shown in parentheses.

Table 3 Scaling coefficients found for each wood type for the relationships shown in Figs 1–5

Relationship (figure)	Temperate diffuse-porous	Tropical diffuse-porous	Ring-porous	Conifer
Conduit diameter vs frequency (Fig. 1)	-2.9 ^a	-2.6	-2.0	-1.6
Stem diameter vs conduit diameter (Fig. 2a)	0.41	0.61	0.59	0.44
Stem diameter vs stem conductivity (Fig. 2b, SMA)	2.9	3.1	4.3	3.2
Stem diameter vs stem conductivity (model analysis, OLS) ^b	2.7	2.6	3.8	1.9
Stem diameter vs leaf area (Fig. 3a)	2.0	1.9	2.2	2.4
Stem diameter vs leaf specific conductivity (Fig. 3b)	1.4	2.0 ^c	2.7	1.3
Hydraulic diameter vs K_{tr} /conduit (Fig. 4a)	5.4	4.9	5.3	3.8
Hydraulic diameter vs K_{tr} /sapwood area (Fig. 4b)	3.7	3.3	4.5	3.0
Hydraulic diameter vs K_{tr} /stem area (Fig. 4c)	3.7	3.5	4.3	3.1
Trunk diameter vs stem conductance (Fig. 5) ^d	1.8	1.8	2	1.2

SMA, standard major axis.

^aAll scaling exponents are significant at $P \leq 0.001$ unless otherwise indicated.

^bOrdinary least-squares (OLS) regression parameters were used to estimate relationships for the model analysis (see the Materials and Methods section for details).

^cSignificant at $P = 0.002$.

^dThese scaling coefficients are for the linear portion of the curve.

taper and the maximum conduit size in the trunk segments. Differences in SMA slopes and intercepts indicate that the maximum conduit size and taper were not, in the main, caused by differences in plant size. This result was confirmed by ANCOVA-adjusted mean conduit diameters (data not shown), which account for differences in stem

diameter and were within $5 \pm 4\%$ of nonadjusted means (Table 2). Ring-porous and tropical diffuse-porous saplings developed the largest vessels in their trunks and showed the greatest conduit taper: a fourfold increase in vessel diameter moving from branches to trunks when calculated for a terminal branch of 0.2 cm and a trunk of 2 cm diameter. The

slopes and intercepts of the SMA lines were not different between these two groups ($P > 0.5$). Conifers had the narrowest conduits with less taper: only a 2.6-fold increase in diameter from branch to trunk over the same stem diameter range. Temperate diffuse-porous trees were intermediate in conduit size and their rate of taper did not differ from conifers ($P = 0.9$). When the taper functions of the *Robinia* individuals from the Oregon and Minnesota sites were compared, no differences were found ($P = 0.44$).

Trends in conduit size and taper were consistent with trends in stem K_h (Fig. 2b). Ring porous K_h increased more than did the other groups with stem diameter (log–log slope = 4.3; $P < 0.001$), consistent with their greater conduit taper. For diffuse-porous species, the rate of increase of K_h with stem size was lowest for the temperate trees (slope = 2.9; $P < 0.001$) but similar to the conifers for the tropical species (slope = 3.2 for conifers, 3.1 for tropical species; $P < 0.001$ for each).

In contrast to the differences between groups in stem hydraulics observed here, sapling leaf areas scaled very similarly with stem size across all groups (Fig. 3a). As a result, the differences in stem K_h between groups translated into

similar differences in leaf-specific conductivity ($K_L = K_h/\text{leaf area}$; Fig. 3b). Ring-porous stems had the highest K_L , particularly at larger stem diameters, and increased more with stem size relative to other groups ($P \leq 0.04$); conifers had the lowest K_L values, and both diffuse-porous groups were intermediate. The functional surface area for the conifers was assumed to be double-sided, which resulted in a halving of the K_L relative to a single-sided leaf area estimate. However, even if this assumption were not completely valid for each species, doubling K_L values would leave the conifers with the lowest estimates. The slopes for the conifers and temperate diffuse-porous species were not statistically different from each other ($P = 0.5$), although they differed from the tropical ($P < 0.02$) and ring-porous species ($P < 0.001$).

In terms of efficiency, greater hydraulic conduit diameter corresponded with increased conductivity at all scales examined (Fig. 4). Both conifer and pooled angiosperm slopes were no different than 4, consistent with an approximately constant offset from the HP line within tracheid and vessel conduit types. This offset can be attributed to additional flow resistance in conduit end-walls. However, within each angiosperm subgroup, slopes were significantly steeper than

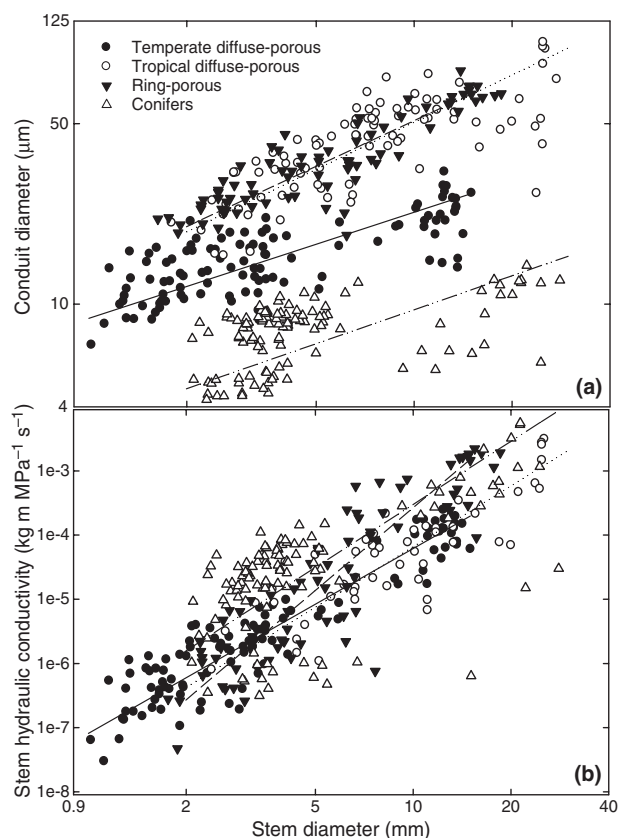


Fig. 2 Conduit diameter (a) and hydraulic conductivity (b) vs stem diameter. Each point represents one branch or trunk segment. Standard major axis (SMA) analyses ($P < 0.001$) are shown for each group: temperate diffuse-porous (solid); tropical diffuse-porous (dotted); ring-porous (dashed); conifers (dash-dot-dotted).

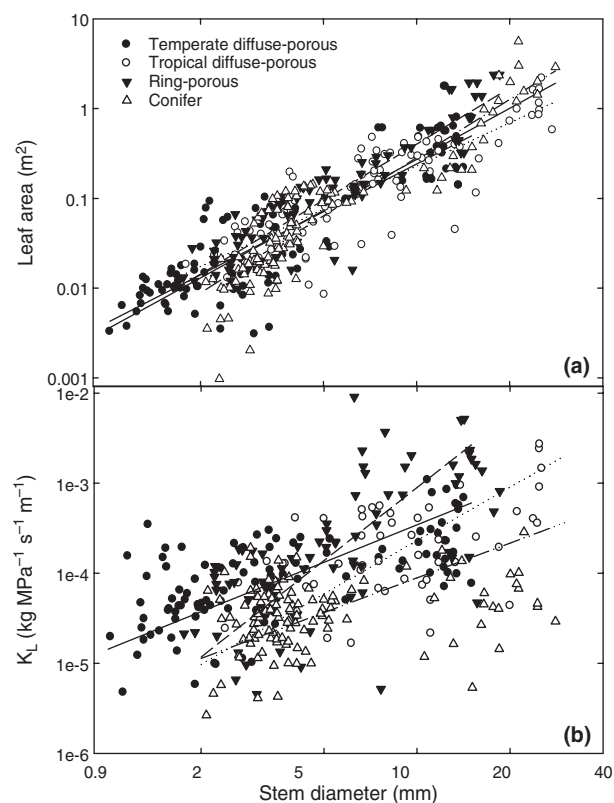


Fig. 3 Leaf area (a) and leaf-specific conductivity (K_L) (b) vs stem diameter. Each point represents one branch or trunk segment. Lines show standard major axis (SMA) analyses ($P < 0.001$), and different lines indicate groups as follows: temperate diffuse-porous (solid); tropical diffuse-porous (dotted); ring-porous (dashed); conifers (dash-dot-dotted).

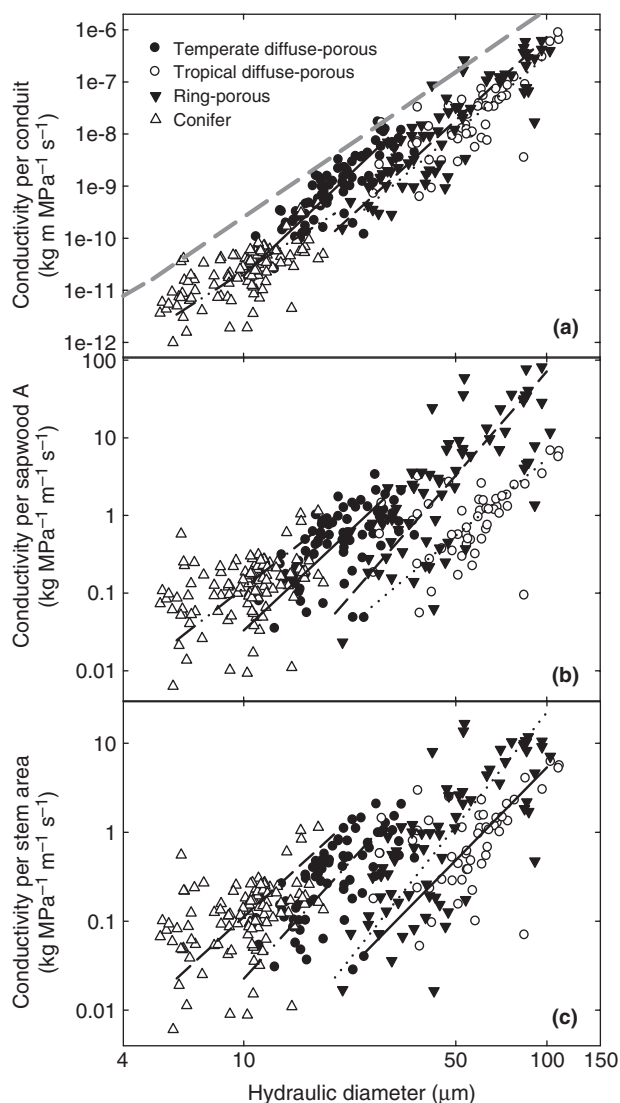


Fig. 4 Conduit-specific (a), sapwood area-specific (b), and stem area-specific (c) conductivity vs mean hydraulic diameter. Each point represents one branch or trunk segment. Solid lines show standard major axis (SMA) analyses ($P < 0.001$), and different lines indicate groups as follows: temperate diffuse-porous (solid); tropical diffuse-porous (dotted); ring-porous (dashed); conifers (dash-dot-dotted). The dashed gray line in (a) is the theoretical conductivity from the Hagen–Poiseuille equation.

4 ($P < 0.001$), indicating that wider vessels of a subgroup experienced less of an HP offset (or end-wall limitation) than narrower vessels. Across all groups, conduits averaged $18 \pm 19\%$ of the theoretical maximum conductivity per conduit diameter given by the HP equation (Fig. 4a, dashed HP line, slope = 4). However, conifers as a group tended to be less efficient on this basis, averaging $14 \pm 15\%$ as compared with $21 \pm 21\%$ for angiosperms (t -test, $P = 0.002$). This result suggests that the flow resistance through conduit end-walls is more of a limiting factor for single-celled tracheids than for multicellular vessels.

When conductivity was expressed on a sapwood area basis, trends in conduit frequency (number per area) have an influence on conducting efficiency. Conifers, with greater conduit frequency, increased their conductivity relative to the angiosperms when expressed on a sapwood area basis (Fig. 4b). Ring-porous species showed a steeper increase in sapwood-specific conductivity with vessel diameter than did conifers or tropical diffuse-porous species ($P \leq 0.05$), but were only marginally steeper than temperate diffuse-porous species ($P = 0.1$). The ring-porous group also achieved the greatest absolute conductivities. The steepness of the ring-porous slope was consistent with this group having a shallower packing slope (Fig. 1), which gives them more large conduits per area than diffuse-porous wood types. However, when the conductivity was expressed on a whole-stem area basis, ring-porous stems were not uniformly more efficient than diffuse-porous ones (Fig. 4c), because a smaller fraction of the total wood area is functional in ring-porous trees.

When stem by K_h scaling (Fig. 2b) was used to estimate tree-sized stem network conductances, a power-function relationship emerged between stem-network conductance and trunk diameter for large networks (Fig. 5; cf. linear regression (gray line) with model output for ring-porous networks (dashed line)). The model indicated major differences in the magnitude and scaling of network conductance between ring-porous, conifers, and diffuse-porous groups. The high K_h and taper in ring-porous saplings translated into the greatest network conductance and the steepest increase with basal area (Fig. 5, ring-porous log–log slope = 2.00). Ring-porous network conductance increased isometrically with trunk area (or with trunk diameter²), indicating the absence of any path-length effect on shoot conductance. The model indicated that a scaling exponent of 3.83 or higher in a plot of K_h vs stem diameter was necessary to

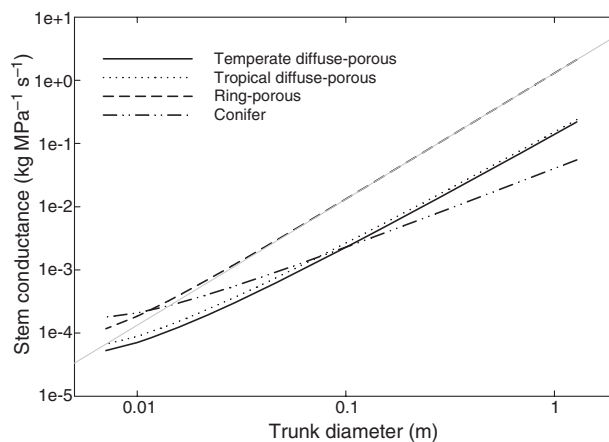


Fig. 5 Calculated stem network conductance vs basal area. The relationship becomes a power function for larger networks as illustrated by the linear regression superimposed on the ring-porous model output (gray line).

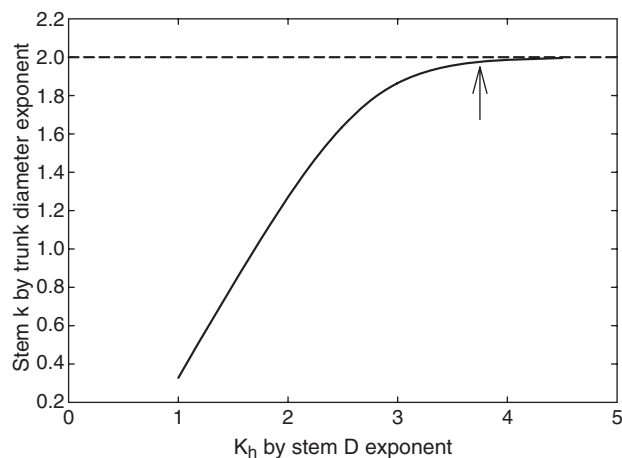


Fig. 6 Scaling exponent from log–log hydraulic conductivity (K_h) vs stem diameter (D) plot (e.g. Fig. 2b) vs the scaling exponent from log–log stem hydraulic conductance (k) vs stem basal area plot (e.g. Fig. 5). The dashed line corresponds to isometric scaling of conductance and basal area. The function asymptotes at isometry, and the arrow indicates the scaling exponent for the x-axis = 3.83 (y-axis = 0.99) that was used to compare with empirical slopes (Fig. 2b) to determine if conductance scaled isometrically in the four groups.

approach a network scaling exponent of 2 (k vs trunk diameter exponent ≥ 1.99) and eliminate the path-length effect (Fig. 6, dashed horizontal line). Conifers, with their lower K_h and conduit taper, had the lowest modeled network conductances at large trunk diameters, which also increased much less with trunk diameter (Fig. 5, conifer power-function slope = 1.2). The intermediate K_h and taper characteristics of diffuse-porous anatomy resulted in stem networks of intermediate modeled conductances and scaling (Fig. 5, temperate and tropical = 1.8, both values less than 2 ($P \leq 0.02$)), indicating significant path-length effects in these groups.

Discussion

The scaling relationships demonstrated in this study show that differences among functional wood types have key effects on the scope and efficiency of water transport and implications that propagate to the network level. The hydraulic traits of all groups scaled differently from each other with respect to size and structural variables. These relationships provide a framework for modeling network transport throughout the individual. The backbone of this framework is the packing function (Fig. 1) and the taper function (Fig. 2a). When combined with the scaling of sapwood area with stem size, these functions dictate how stem conductivity scales with stem size (Fig. 2b), and hence the scaling of the entire stem network conductance for a given (WBE) branching architecture (Fig. 5).

The underlying significance of the packing and taper functions is highlighted by the variation among groups. For the packing function, the offset from the packing limit is

necessary to accommodate strength and storage requirements, yet a greater offset reduces conducting capacity (Zanne *et al.*, 2010). Fewer, wider conduits are theoretically more efficient than more, narrower ones (Zanne *et al.*, 2010). Therefore, more efficient networks, such as ring-porous ones, will be further to the right on the packing function slope than less efficient ones, like the conifers (Figs 1, 5). The implication of the packing slope is less clear, but should depend on how the limitations of the offset vary with stem size. The shallow slope of the conifers, for example, may be the result of denser wood in twigs compared with the trunk. This shift in wood density may be necessary in part to avoid implosion of tracheids caused by the increasingly negative pressures experienced further along the hydraulic path (Hacke *et al.*, 2001; Koch *et al.*, 2004; Domec *et al.*, 2008). The packing function slope will also influence velocity gradients as water moves from the bottom to the tops of trees, with slopes less negative than -2 contributing to accelerating velocity moving from trunk to branch, and vice versa for steeper slopes. However, velocities are also influenced by the sapwood area profile and the functional significance of velocity gradients is ambiguous.

What is the significance of the taper function? A tree would have the highest conductivity for all branch sizes if there were no taper, and if all of the conduits were as wide as the widest trunk conduits. Previous work has focused on the effect of taper on eliminating the decline in conductance with path length (Enquist *et al.*, 2000; Zaehle, 2005; Anfodillo *et al.*, 2006; Mencuccini & Holta, 2007), but all of these analyses ignore the important fact that as conduits become narrower, their number per unit wood area increases (Fig. 1; Sperry *et al.*, 2008). In any event, sacrificing a higher conductance for the sake of eliminating a path-length effect would seemingly put a tree at a competitive disadvantage. Vascular networks that do not contribute to mechanical support, such as in some leaves, in stems of *Psilotum*, and some vines, apparently taper at a rate that optimizes the conductance for a given network volume as predicted by Murray's law (McCulloh *et al.*, 2003; McCulloh & Sperry 2005; McCulloh *et al.*, 2009). But the Murray law optimization criteria do not consider a mechanical-support function for vascular tissue and so the law does not apply to the secondary xylem of free-standing trees. Nor do trees conform to the taper rates predicted by Murray's law (McCulloh *et al.*, 2004).

An alternative explanation for taper is that not enough 'trunk-sized' conduits can fit into small-diameter branches. The negative pressure system of the xylem is inherently dangerous and requires the redundancy of multiple pipes in parallel (Ewers *et al.*, 2007). To achieve the necessary redundancy as stem xylem areas decrease from trunk to twig, conduits may have to become narrower simply to fit, in sufficient numbers, in the shrinking available space. In addition, narrower twig conduits may also be more cavita-

tion-proof (Hacke *et al.*, 2006) or easier to refill, and the damping of a path-length effect on conductance may aid the equitable distribution of resources within the branches of an individual (Zimmermann, 1978; Tyree *et al.*, 1983; Ewers & Zimmermann, 1984a,b).

The extent of taper is obviously influenced by the maximum vessel size produced by the trunk (Fig. 2a), a parameter that is strongly tied to wood type and habitat. A clear example of this link is that the temperate diffuse-porous trees developed much narrower vessels than their tropical counterparts (Fig. 1). The functional basis for smaller temperate vessels is likely tied to their greater protection from cavitation by freeze–thaw events (Baas, 1986). Davis *et al.* (1999) found that stems from species with mean vessel diameters greater than *c.* 30 μm experience nearly complete loss of hydraulic function when subjected to a relatively mild xylem tension during one freeze–thaw cycle. Species with narrower conduits did not lose function. Of the 112 stems from temperate diffuse-porous saplings examined here, none had a mean vessel diameter > 30 μm (Fig. 1, dotted vertical line). More mature diffuse-porous stems may have mean vessel diameters that exceed this threshold value, and may either refill them in the spring or rely on a large sapwood area containing vessels of a variety of sizes (Sperry & Sullivan, 1992).

The temperate ring-porous species also experience freeze–thaw events, but exhibit mean vessel diameters > 30 μm and tolerate the freezing-induced dysfunction by relying heavily on newly created vessels each spring. Some evidence suggests ring-porous species may be able to refill vessels overnight (Taneda & Sperry, 2008) and perhaps they are able to refill some of the previous year's vessels each spring. Dye ascent showed more than one functional ring in the trunks of the ring-porous species examined here, and tyloses (outgrowth of parenchyma cells that block axial flow through vessels) were not observed in the most recent 3–4 yr of growth (data not shown). The tracheids of temperate conifers are also at risk of embolisms induced by freeze–thaw (Pittermann & Sperry, 2006), but tracheid size is probably most constrained by their need to be mechanically competent to hold up the tree as well as conduct water (Pittermann *et al.*, 2006).

Conduit diameter is only one of two determinants of its conducting capacity. The other component is how close the conduit comes to achieving its theoretical maximum conductivity (Fig. 4a). All conduits fall far short because of the high resistivity of the interconduit pits (Choat *et al.*, 2008) and, potentially for some angiosperms, also in the perforation plates between vessel elements. The single-celled tracheid of conifers suffers the most because its short length forces water to cross pits more frequently. Nevertheless, it is remarkable that the tracheids do as well as they do compared with angiosperm vessels, owing to their more efficient torus-margo pitting (Pittermann *et al.*, 2005). Within the angiosperms studied, all species except one exhibited simple perforation plates, while *A. rubra* has scalariform plates.

Although scalariform plates from several species have been shown to greatly reduce conductance relative to simple plates (MC Christman & JS Sperry, unpublished; Schulte *et al.*, 1989; Sperry *et al.*, 2007), *A. rubra* did not have lower conductivity per vessel than the other temperate diffuse-porous species ($P = 0.1$). This species may have longer vessels for a given diameter than other species in order to compensate for the greater friction of the plates, or it may have a more conductive plate morphology.

Although our results indicate considerable variation in how network conductance scales with trunk diameter, the actual links between conductance allometries, plant height growth and ultimately plant fitness and ecosystem productivity are complicated (Eamus, 2003; Ryan *et al.*, 2006). Our model results indicate that conifers may perform the worst from a hydraulic standpoint as they grow (Fig. 5). Not only do they exhibit the strongest path-length effect as conifers grow taller, but they also exhibit the lowest absolute values of stem conductance. This result seems incongruous with their being the tallest plants on earth (Koch *et al.*, 2004; Domec *et al.*, 2008). However, differences in factors not considered here, such as leaf and root system hydraulic architectures and departures from WBE branching architecture, will have an impact on network conductance. Resources aside from water (such as nutrients and carbon) may also influence shoot allometry both independently of and interactively with hydraulic considerations. Relationships between hydraulic efficiency and hydraulic safety also influence species- and site-specific maximum height asymptotes (Domec *et al.*, 2008; Sperry *et al.*, 2008). Furthermore, there is little empirical evidence that declines in whole-tree conductance relative to total tissue mass are sufficient to limit tree carbon budgets and height growth (Ryan *et al.*, 2006).

Our results also have important implications for metabolic scaling theory (Brown *et al.*, 2004). The original WBE model (West *et al.*, 1999) assumes that the metabolic rate of a tree is proportional to its hydraulic conductance, and predicts isometric scaling between stem conductance and basal area (slope of 2 in Fig. 5) as required to eliminate a path-length effect. This result leads to a prediction that metabolic rate will be proportional to stem mass (M) to the power of 0.75. This prediction assumes that M is proportional to volume, and volume is proportional to D^2H , where D is trunk diameter and H is tree height. If H is proportional to $D^{0.67}$ (elastic similarity), then M is proportional to $D^{2.67}$. If metabolic rate is proportional to conductance, which is proportional to D^2 (i.e. basal area), then it is proportional to $M^{2/2.67} = M^{0.75}$. If we use q to represent the scaling exponent for conductance by D (log–log slopes in Fig. 5; Table 3), then metabolic rate would be proportional to $M^{0.375q}$.

Of the four groups analyzed here, only the ring-porous species showed isometric scaling of network conductance with basal area (conductance-by-trunk diameter scaling

exponent in Fig. 5 of $q = 2.00$). Under the assumptions of the WBE model, this exponent would result in the metabolic rate being proportional to $M^{0.75}$. The network conductances of the conifers and both diffuse-porous groups scaled less than isometrically with basal area. Their scaling exponents imply that metabolic rate should be proportional to $M^{0.45}$ in conifers ($q = 1.2$), and to $M^{0.68}$ in the two diffuse-porous groups ($q = 1.8$). These relationships apply to large networks where conductance scaling was log-linear; fitting a power function to smaller networks would decrease the predicted conductance and M exponents (Fig. 5). These differences from the predictions of the metabolic scaling theory were observed even though the assumptions about branching architecture used here were the same as those used by the WBE model. These results suggest that there is no universal scaling exponent for the relationship between metabolic rate and plant body mass, but instead that the underlying packing and taper functions create a spectrum of exponents that also exhibit ontogenetic shifts.

Variable scaling is, in fact, what is seen in empirical studies. Measurements of whole-tree conductance show less than isometric scaling with basal area (Mencuccini, 2002; Sperry *et al.*, 2008) as we saw with three of the four wood types. There is also evidence that conductance may begin to saturate in large-diameter trees (Meinzer *et al.*, 2005). These observations are consistent with conductance scaling with stem mass below the 0.75 WBE exponent. Mencuccini (2002) found conductance-by-mass exponents of 0.63 and 0.64 for two species of diffuse-porous *Acer*, similar to what we predict for this group (0.68). He found even lower exponents for two species of *Pinus* (0.4 and 0.44), again similar to our result of 0.45 for conifers.

Other studies suggest that hydraulic conductance-by-mass scaling is not identical to metabolism-by-mass. A meta-analysis of respiration rate of temperate species found that it scaled with $M^{0.84}$ (Reich *et al.*, 2006), which is roughly the same degree higher than the hypothetical $M^{0.75}$ as the conductance-by-mass scaling was lower in the diffuse-porous groups.

Size-dependent shifts in scaling exponents are actually consistent with the underlying structure of the original WBE model, as shown recently (Savage *et al.*, 2008). However, the WBE vascular architecture contradicts the packing function (Sperry *et al.*, 2008). A revised metabolic scaling model that is based on the packing function has recently been completed (VM Savage, LP Bentley, BJ Enquist, JS Sperry, PB Reich, and EE VonAllmen, unpublished data). Future work must also address the importance of external branching structure on scaling theory, expanding from the deliberately simple architecture currently employed in the WBE framework. Additional refinements may be needed to better link the model predictions of water flux to metabolic processes (Reich *et al.*, 2006).

The suite of traits comprising a plant's hydraulic architecture is the result of both its evolutionary history and compensatory adjustments to its environment. The observed differences in the conducting capacity of functional wood types derive from the packing and taper function differences that propagate to the network level and jointly are associated with variation in daily (Bush *et al.*, 2008; Taneda & Sperry, 2008) and seasonal cycles of water use (Vogt, 2001), and presumably carbon gain and growth. The functional consequences of structural limitations caused by environmental stresses, such as freeze–thaw events, are highlighted when compared across habitats. However, to fully understand how hydraulic architecture influences temporal and ontogenetic differences in whole-plant function across a range of habitat types, the effects of branching architecture need to be addressed, as well as the contributions of roots and leaves.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 ANOVA results testing sources of variation in anatomical characteristics

Table S2 Standard major axis (SMA) analyses showing slopes for the comparison of conduit diameter vs frequency.

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