



Axial variation of xylem conduits in the Earth's tallest trees

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Abstract

Key message In the Earth's tallest tree species, axial variation in conduit size matches theoretical predictions minimizing the accumulation of hydraulic resistance with height growth, within a constraint of maximum conduit diameter.

Abstract Hydraulic limitations to tree height can be mitigated by widening the conducting elements toward a tree's base. However, size limits of tracheid and vessel dimensions may constrain this compensation mechanism as the water transport pathway elongates. Moreover, variation in conduit size is poorly described in tall trees even though their long transport paths have high potential for hydraulic resistance. Here, we evaluated whether axial variation in conduit diameter was uniquely structured, or matched theoretical predictions in *Sequoia sempervirens*, *Sequoiadendron giganteum*, and *Eucalyptus regnans* that were 86–105 m tall and exceeded 85% of the maximum height for each species. Across *Sequoia* and *Sequoiadendron*, tree top tracheids maintained constant width, whereas tree base tracheids in the outermost ring were 20% wider in taller trees, suggesting maintenance of basipetal conduit widening with height growth. In all trees, the observed widening decreased at a rate per unit path length that fitted well to a power function with an exponent consistent with hydraulic compensation. However, below about 60 m from the tree tops, conduit diameters approached an asymptote beneath the power function, indicating a limit to maximum conduit size. Quantifying the distribution of base-to-top hydraulic resistance suggested that the minimal hydraulic benefit gained with increasingly wider conduits near the tree base may trade off with other factors such as maintaining mechanical strength or reducing fluid volume. We summarize these results into an anatomical model of height growth that includes limits to axial variation in conduit diameter and is supported by many physiological and anatomical observations.

Keywords Coast redwood · Giant sequoia · Hydraulic resistance · Metabolic scaling theory · Mountain ash · Tall trees · Tree height growth · Wood anatomy

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Introduction

The rate of height growth decreases as trees approach their maximum height (Ryan and Yoder 1997). The possible reasons for this decline are generally focused on mechanical or physiological limitations (Friend 1993; Niklas 2007; Sala and Hoch 2009). In recent years, the hydraulic limitation hypothesis (Ryan and Yoder 1997; Ryan et al. 2006) proposed that taller trees experience slower height growth due to two compounding factors: (1) the greater effect of the gravitational potential gradient that imposes -0.01 MPa per meter of height, and (2) longer water transport paths and thus more hydraulic resistance through the xylem conduits. Both factors constrain height growth via reduced minimum leaf water potentials that inhibit turgor pressure (Woodruff et al. 2004), leaf expansion (Oldham

et al. 2010), and photosynthesis (Tezara et al. 1999). Indeed, maximum height in the tallest conifers *Sequoia sempervirens* and *Pseudotsuga menziesii*, as estimated via limits to shoot functional characteristics imposed by gravity and hydraulic resistance, was consistent with historical height records (Koch et al. 2004; Domec et al. 2008). Assessment of the hydraulic limitation hypothesis revealed compensation mechanisms that mitigate the accumulation of hydraulic resistance with tree height growth, including varying the dimensions of the xylem conduits along the hydraulic pathway (Anfodillo et al. 2013; Olson et al. 2018), but whether axial variation in conduit diameter is uniquely structured in the Earth's tallest trees remains to be evaluated.

A number of prominent plant vasculature optimality models balance hydraulic efficiency against embolism risk, mechanical constraints, and/or construction costs (Rosell et al. 2017), although not all are applicable to a wide diversity of plants. For example, Murray's law (Murray 1926) maximizes the conductance through the vascular system per investment in transport tissue by equalizing the sum of the conduit radii cubed at all points along the hydraulic pathway, resulting distally in a larger number (i.e., furcation) of narrower conduits, but the assumption that the conduits do not serve a structural support function renders this model overly simplistic for the diffuse-porous and conifer woods (McCulloh et al. 2003; McCulloh et al. 2004) produced by the tallest trees. Other models that optimize carbon gain while maintaining transport safety and efficiency may be more broadly applicable (Mencuccini et al. 2007; Hölttä et al. 2011), but they have not considered the mechanical strength necessary to resist buckling or the space-filling constraints on packing conduits into a stem that other models centered on hydraulic optimality have included (West et al. 1999; Savage et al. 2010).

A common theme in these models is that each conduit in the series is slightly narrower than the next, such that the series tapers toward the apex (Sanio 1872; Fegel 1941; Zimmermann 1978). Natural selection should theoretically favor base-to-top conduit tapering because wider conduits counter the increase in hydraulic resistance due to longer hydraulic paths as described by laminar flow in the Hagen–Poiseuille equation:

$$r = \frac{128\mu L}{\pi D^4}, \quad (1)$$

where r = hydraulic resistance, μ = dynamic viscosity (fixed for water at a given temperature; e.g., $\mu = 1.002$ mPa at 20 °C), L = path length, and D = conduit diameter (Tyree and Zimmermann 2002). In Eq. 1 note that for a constant diameter, increasing path length has an additive effect on resistance, while for a constant length, increasing conduit

diameter exponentially reduces r . Therefore, a vertical profile of conduits that increases in diameter basally, referred to herein as “basipetal widening”, compensates for the addition of r that would otherwise accumulate as trees grow taller (Anfodillo et al. 2013; Olson et al. 2018).

Basipetal conduit widening is a central tenet of metabolic scaling theory (MST), a theoretical framework mechanistically linking organism size to individual, community, and ecosystem attributes (West et al. 1999). For individual vascular plants adhering to MST, metabolic processes are optimized if certain assumptions—a volume-filling, fractal-like hierarchical branching architecture with no conduit furcation; invariantly sized leaves; uniform biomechanical constraints; and minimization of r —are met (Enquist 2002). This framework yielded the prediction that basipetal conduit widening should follow a power function with a characteristic exponent (Anfodillo et al. 2006):

$$D = \alpha L^\beta, \quad (2)$$

where D = conduit diameter, L = distance from tree top, α = scaling coefficient (i.e., y-intercept), and β = scaling exponent (i.e., slope). The rate of basipetal widening is described by β . A zero value indicates conduits of uniform diameter as in the pipe model (Shinozaki et al. 1964), whereas larger values indicate greater rates of widening. Importantly, at $\beta \geq 0.20$ MST predicts that r becomes nearly independent of L , and that the reduction in conductance per leaf area, risk of cavitation, and costs of construction are all minimized with stem elongation (West et al. 1999; Enquist 2003; Anfodillo et al. 2006; Petit and Anfodillo 2009; Rosell et al. 2017). Therefore, according to MST, $\beta = 0.20$ can be considered a minimum threshold above which metabolic efficiency may be maintained throughout tree height growth (Enquist 2003).

An important implication of MST is that a tree could grow taller without accumulating much additional r , which is inconsistent with the hydraulic limitation hypothesis (Ryan and Yoder 1997; Ryan et al. 2006). Vigorous debate has surrounded the MST (Coomes 2006; Martinez del Rio 2008)—its underlying premise has been questioned (Glazier 2015) and its assumptions challenged (Kozłowski and Konarzewski 2004). That r could be virtually independent of hydraulic path length has even been highlighted as maladaptive because saplings would be penalized (McCulloh and Sperry 2005), and there is skepticism about whether a specific threshold of basipetal conduit widening can minimize r with height growth (e.g., Hacke et al. 2016; Pfautsch 2016). Correct or not, the MST has brought a new focus on several functional implications of axial variation in conduit dimensions. Basipetal conduit widening across a broad array of woody angiosperms and conifers fits well to a power function and yields β converging to about 0.20 (Anfodillo et al. 2013; Olson et al. 2018). It reduces the accumulation of r

with height growth (Becker et al. 2000) and concentrates the vast majority of r toward a tree's top where conduits are narrowest (Tyree and Zimmermann 2002; Petit et al. 2008, 2010), but it cannot fully render r independent of hydraulic path length (Mäkelä and Valentine 2006). In addition, larger β values (e.g., 0.30) markedly reduce total r (Becker et al. 2000), but limitations to minimum tree top and maximum tree base conduit diameters may constrain β .

Constraints to β should be apparent in conduit sizes at the tree top and base, such that apical conduits widen and basal conduits narrow with height growth, or that conduit widths at these positions are uncorrelated with tree height. Conduit width at the tops of tall conifers is probably constrained by small pits that increase safety from cavitation but also dramatically impede water flow (Domec et al. 2008; Lazzarin et al. 2016). Indeed, taller angiosperms produce wider conduits at the tree apex relative to the apical conduit diameters found in shorter species, so taller trees can supply the leaves with the same amount of water using a smaller number of wider conduits (Olson et al. 2014, 2018). Developmentally, conduit dimensions at the tops of tall trees are likely influenced by gravity, which imposes low water potentials, and in the absence of complete osmotic compensation, low turgor pressures that may limit cell expansion (Woodruff et al. 2004). At tree bases, maximum conduit size is sometimes evident as diameters approach an asymptote both radially from inner to outer growth rings (Spicer and Gartner 2001; Leal et al. 2007) as well as axially from tree top to base (Becker et al. 2003; James et al. 2003; Anfodillo et al. 2006; Mencuccini et al. 2007; Petit et al. 2010). Reasons for the upper limits to tree base conduit diameter remain unclear but may be related to mechanical strength (Pittermann et al. 2006a; Sperry et al. 2008), the greater risk in wider conduits of embolisms forming during freeze–thaw events (Pittermann and Sperry 2003; Mayr and Sperry 2010), or minimizing fluid volume to maintain an efficient distribution network (Banavar et al. 1999). Limits to tree top and tree base conduit diameters have implications for basipetal conduit widening as a hydraulic compensation mechanism because they translate to increased r via smaller β as trees grow taller. Thus, descriptions of axial variation in conduit widths in exceptionally tall trees provide a foundation to evaluate constraints on basipetal conduit widening as a hydraulic compensation mechanism.

Variation in conduit diameter must co-occur with changes in conduit length and pit structure to prevent any single component from generating a disproportionate amount of the total conduit r (Choat et al. 2008); inferring whole-conduit r from lumen-only measurements requires constant proportionality between lumen and end-wall r . Direct empirical support for such proportionality has been provided among species (Hacke et al. 2006; Wheeler et al. 2005; Pittermann et al. 2006b) and presumably applies intraspecifically

because of the positive relationships between vessel length and diameter, pit membrane area and lumen size, and between pit size and pit porosity observed within several species (Domec et al. 2008; Lazzarin et al. 2016; Jacobsen et al. 2018a). This presumed proportionality between lumen and pit r facilitates investigations into the implications of axial variation in conduit diameter on r because lumen diameter is much easier to quantify than pit structure. Moreover, combined measurements of conduit diameter and r strongly suggest that basipetal conduit widening mitigates path length r and show that the rate of r accumulated with path length is indeed predictable from anatomical measurements (Petit et al. 2008).

Despite the many theoretical developments and empirical data of tree hydraulic architecture advanced in recent years, we have a poor understanding of how well current theory applies to nature's extremes; the power of the MST to predict axial variation in conduit size in tall trees remains insufficiently tested. Our objective was to evaluate whether axial variation in conduit diameter in exceptionally tall trees is uniquely structured, or matches theoretical predictions as has been well documented in shorter trees. Study species included the 1st and 4th tallest conifers, *Sequoia sempervirens* and *Sequoiadendron giganteum*, as well as the tallest angiosperm *Eucalyptus regnans*. We predicted the rate of basipetal conduit widening to be ≥ 0.20 as an indicator of hydraulic compensation with height growth, and we evaluated how apical and basal conduit dimensions might influence whole-tree hydraulic efficiency.

Materials and methods

Study sites and trees

Study sites were selected based on the abundance of exceptionally tall trees for a given species. Humboldt Redwoods State Park, California, along the floodplain of Bull Creek (40°N, 124°W; 45–65 m elevation) contains a high proportion of the Earth's tallest trees (Sawyer et al. 2000). Four *Sequoia sempervirens* (D. Don) Endlicher ranging in height from 99 to 105 m were selected for study there in 2013. Tall *Sequoiadendron giganteum* (Lindley) J. Buchholz occur in scattered groves in California's Sierra Nevada Mountains (Willard 2000). In 2013, we selected three *Sequoiadendron* that were 87 m tall from Calaveras Big Trees State Park (38°N, 120°W; 1450–1470 m elevation) as well as three additional trees that were 90 to 95 m tall from Kings Canyon National Park and neighboring Whitaker's Forest Research Station (37°N, 119°W; 1670–1780 m elevation). Wallaby Creek on the Hume Plateau in Kinglake National Park, Victoria, Australia (37°S, 145°E; 450–500 m elevation) hosted

the tallest angiosperm forest before the stand-replacing Black Saturday Fire (Cruz et al. 2012) swept through the understory on 7 February 2009, killing all overstory trees but leaving their fine twigs intact (Sillett et al. 2015a). We selected five of these dead *Eucalyptus regnans* F. von Mueller that were 86 to 93 m tall for collection of wood specimens in 2010. All study tree heights were > 85% of the tallest known individual for a given species and included the second tallest known *Sequoiadendron* and *Eucalyptus* (Table 1).

Wood specimen collection

We climbed each study tree using rope techniques (Jepson 2000) to access the entire length of the main stem axis (i.e., trunk). Total tree height (H) was established by lowering a fiberglass measuring tape from the tree top to average ground level. All heights were recorded to cm resolution. In *Sequoia* and *Sequoiadendron*, a 12-mm-diameter increment borer was used to extract cores from the trunk of each tree, while in the dead *Eucalyptus* chainsaws were used to extract wedges. Cores and wedges captured the outermost five annual rings. We avoided the swollen bases of the trees as well as branch junctions, burls, and other structural anomalies to reduce the probability of encountering reaction wood. Wood specimens were collected at 5–10-m intervals along the lower half of the trunk and at increasing frequencies closer to the tree top to capture the rapid change in conduit diameter expected near the apex. Collection heights were later converted to distance from tree top (L) to enable comparisons among trees of different heights during analyses.

Extraction of wood anatomical data

Quantitative data describing conduit size along the trunks were extracted using a rigid, standardized protocol to minimize measurement errors (von Arx et al. 2016). Transverse sections of each core or wedge were carved from the field specimens, softened in hot water, and sectioned (12–15 μm) using a disposable blade mounted to a sliding Reichert microtome. These thin sections were then stained with 1% safranin and permanently mounted to glass microscope slides using Eukitt (Bioptica, Milan, Italy). Each mounted section was viewed under a light microscope (Eclipse 80i; Nikon Instruments Inc., Tokyo, Japan) through which the outermost annual ring was photographed with a digital camera. We analyzed the digital images with ImageJ v. 1.45d (Rasband 1997–2019) to quantify the areas of at least 20 vessels (in *Eucalyptus*) or 100 tracheids (in *Sequoia* and *Sequoiadendron*) with 0.0001- μm^2 resolution in a zone of the transverse section that included the outer complete growth ring between two rays. Lumen areas (A) were converted to diameters (D) by assuming circular cross sections and using the formula $D = 2(A/\pi)^{1/2}$.

Data analysis

Before analyzing variation in conduit diameter, we reduced the probability of including the tapered ends of xylem conduits by removing those with a diameter less than half of the largest lumen within each annual ring's radial profile (James et al. 2003). We then calculated hydraulic mean diameter (D_h), which accounts for each conduit's contribution to hydraulic conductance for the N conduits within an annual ring:

$$D_h = \frac{\sum_{n=1}^N D_n^5}{\sum_{n=1}^N D_n^4}, \quad (3)$$

Table 1 Names, locations, and sizes of 15 *Sequoia sempervirens*, *Sequoiadendron giganteum*, and *Eucalyptus regnans* study trees

Name	Species	Location	DBH (m)	Height (m)
SESE 1	<i>Sequoia sempervirens</i>	Humboldt Redwoods State Park	3.31	104.8
SESE 2	<i>Sequoia sempervirens</i>	Humboldt Redwoods State Park	3.39	104.6
SESE 3	<i>Sequoia sempervirens</i>	Humboldt Redwoods State Park	2.30	101.1
SESE 4	<i>Sequoia sempervirens</i>	Humboldt Redwoods State Park	2.42	99.3
SEGI 1	<i>Sequoiadendron giganteum</i>	Kings Canyon National Park	4.21	94.8
SEGI 2	<i>Sequoiadendron giganteum</i>	Whitaker Forest Research Station	4.99	90.7
SEGI 3	<i>Sequoiadendron giganteum</i>	Whitaker Forest Research Station	2.93	90.0
SEGI 4	<i>Sequoiadendron giganteum</i>	Calaveras Big Trees State Park	4.73	86.7
SEGI 5	<i>Sequoiadendron giganteum</i>	Calaveras Big Trees State Park	4.22	86.6
SEGI 6	<i>Sequoiadendron giganteum</i>	Calaveras Big Trees State Park	6.21	86.5
EURE 1	<i>Eucalyptus regnans</i>	Kinglake National Park	2.65	92.6
EURE 2	<i>Eucalyptus regnans</i>	Kinglake National Park	3.12	91.5
EURE 3	<i>Eucalyptus regnans</i>	Kinglake National Park	2.74	87.7
EURE 4	<i>Eucalyptus regnans</i>	Kinglake National Park	2.98	86.8
EURE 5	<i>Eucalyptus regnans</i>	Kinglake National Park	2.70	85.7

where D = diameter of lumen n (Sperry and Saliendra 1994). In Eq. 3 is a superior representation of hydraulic conductivity compared to the unweighted mean vessel diameter (Hacke et al. 2016).

All statistical analyses were performed in R (R Development Core Team 2015). We performed reduced major axis (RMA) regression using the R package ‘smatr’ (Warton et al. 2015) to establish the scaling relationships between each set of pairwise comparisons of D_h and L . These two variables were \log_{10} -transformed to linearize their relationship and to comply with assumptions of normality and homoscedasticity prior to regression analyses (Sokal and Rohlf 1995). Regression analyses yielded a scaling exponent (β ; i.e., slope), scaling coefficient (α ; i.e., y-intercept), and 95% confidence intervals, taking the form $\log_{10}Y = \log_{10}\alpha + \beta\log_{10}X$, where $X=L$ and $Y=D_h$. $\log_{10}\alpha$ and its associated 95% confidence interval were then retransformed into the linear scale for reporting as components of a power function with β , taking the form $Y = \alpha X^\beta$ that was fit to each tree’s set of pairwise comparisons. Thus, β represents the rate of change in D_h along the trunk, while α (hereafter, D_{h-top}) represents D_h at 1 cm from the tree top. In addition to calculating D_{h-top} , β , and 95% confidence intervals separately for each tree, we also calculated species-level D_{h-top} and β to narrow confidence intervals and reduce the uncertainty of fit for each species. Confidence intervals that overlapped with $\beta \geq 0.20$ were considered evidence of hydraulic compensation and in agreement with MST (Anfodillo et al. 2006, 2013).

To evaluate limits to conduit size, relationships between H and D_{h-top} as well as between H and extrapolated tree base conduit diameter (D_{h-base}) were analyzed using ordinary least squares regression on \log_{10} -transformed data to determine the significance of slope. Additional anatomical data available for *Eucalyptus regnans* (Petit et al. 2010) enabled us to compare D_{h-top} from three medium-sized trees (average $H=57.3$ m) with our three tallest *Eucalyptus* using a t -test on the scaling coefficients derived via RMA regression.

Hydraulic resistance calculation

To quantify the distribution of hydraulic resistance (r) encountered by a single water molecule traveling from tree base to top (after Petit et al. 2010), we constructed a hypothetical pipeline using axial changes in tracheid diameters and lengths (T_l) for our tallest individual *Sequoiadendron* (SEGI 1, $H=94.8$ m; Table 1). The relationship between T_l and L ($T_l=2.7 L^{0.23}$) was obtained from Lazzarin et al. (2016) for the same individual. The pipeline consisted of a uniseriate series of tracheids stacked end-to-end with the topmost conduit diameter and length equal to α , while the rate of basipetal widening or lengthening was equal to β . Each tracheid was assumed to be cylindrical. Tracheid dimensions below our lowest measurements (i.e., beyond

the largest L of 91.8 m for SEGI 1) were extrapolated from the relationships between D_h and T_l with L to assess how a hypothetical increase in path length would influence the accumulation of r . We then applied the Hagen–Poiseuille equation to calculate r for each conduit, added 67% for tracheid end-wall contributions (Lancashire and Ennos 2002; Pittermann et al. 2006b), and finally summed the accumulation of r with increasing pipeline length. For comparison, we also quantified the accumulation of r using $\beta=0$, $\beta=0.20$, and $\beta=0.25$, as well as using a constant T_l of 1.0 cm.

Results

Axial variation in conduit diameter

In all study trees, D_h was narrowest near the tree top, widened rapidly basipetally, and was widest near the tree base where the conduit diameters increased gradually toward the ground (Fig. 1). Measured values of tracheid D_h in *Sequoia* and *Sequoiadendron* were similar for a given L , ranging from 9.0 μm at $L=0.20$ m to 67.5 μm at $L=84.80$ m. Vessel elements in *Eucalyptus regnans* were much larger, ranging from a minimum of 28.0 μm at $L=0.01$ m to a maximum of 260.7 μm at $L=47.70$ m.

A power function fit well to each set of pairwise comparisons of D_h and L (Fig. 1), explaining 81–98% of the variation when trees were analyzed separately, and 89–95% when grouped by species (Table 2). However, beginning approximately 60 m from the tree tops, the rate of basipetal widening declined below the power function as D_h approached an asymptote (Fig. 1, insets). Scaling exponents (β) describing the rate of D_h widening with L ranged from 0.18 to 0.29 (Table 2) and were within the range commonly reported. Consistent with MST, 95% confidence intervals for β included values ≥ 0.20 for each of the 15 study trees as well as for each of the three species when data were analyzed intraspecifically (Table 2). Scaling coefficients (D_{h-top}) representing D_h at 1 cm from tree top positions were indistinguishable between *Sequoia* and *Sequoiadendron* (two-tailed t -test; $P=0.62$) and ranged from 3.6 to 8.9 μm , while those for *Eucalyptus* were much larger and ranged from 19.2 to 30.1 μm . Extrapolating D_h to tree base positions (D_{h-base}) yielded larger values for *Sequoia* than *Sequoiadendron*, averaging 59.8 and 47.1 μm , respectively, while *Eucalyptus* averaged 266.9 μm .

Conduit diameter and total tree height

Constraints to β should be apparent in limits to D_{h-top} and D_{h-base} , such that D_{h-top} either increases or does not correlate with H , or that D_{h-base} either decreases or does not correlate with H . Since we found no differences in D_{h-top} or β between

Fig. 1 Scaling relationships between tracheid or vessel element hydraulically weighted diameter and distance from tree top for *Sequoia sempervirens*, *Sequoiadendron giganteum*, and *Eucalyptus regnans* trees 86–105 m tall. Each panel is a composite of multiple individuals: *Sequoia*, $n=4$; *Sequoiadendron*, $n=6$; *Eucalyptus*, $n=5$. Inset figures show the same data plotted onto untransformed axes. Dashed envelopes represent 95% confidence intervals. Relationships were derived via reduced major axis regression

Sequoia and *Sequoiadendron*, we combined these two conifers into a single group to expand the range of H among trees to test for changes in D_{h-top} and D_{h-base} with H (Fig. 2). We found no correlation between D_{h-top} and H ($P=0.7889$, $R^2=0.0094$). However, D_{h-base} was positively correlated with H ($P=0.0004$, $R^2=0.8037$). Thus, across the conifers spanning a H range from 86.5 to 104.8 m, apical conduit diameters maintained a constant mean width of 5.6 μm while those among tree bases increased 20% from 44.8 to 61.6 μm . Within our narrow range of H for *Eucalyptus*, we found no correlation between D_{h-top} and H ($P=0.8293$, $R^2=0.0181$) or between D_{h-base} and H ($P=0.6148$, $R^2=0.0945$). However, a t -test comparing average D_{h-top} derived via RMA regression from three medium-sized *Eucalyptus* (Petit et al. 2010) versus our three tallest individuals revealed significantly wider average D_{h-top} in the taller trees (19.9 μm versus 27.1 μm ; $P=0.0235$).

Distribution of within-tree hydraulic resistance

As expected, hydraulic resistance (r) for our tallest individual *Sequoiadendron* (SEGI 1) was highest toward the tree top and lowest at the tree base. Including axial variation in T_l systematically reduced r along the trunk compared to holding T_l constant at 1.0 cm (Fig. 3). Compared to smaller β , the high value of 0.29 for this tree yielded lower total r . Toward the tree base r accumulated slowly, and extrapolating this trend to a hypothetically longer path length suggested that r would not appreciably increase with added tree height.

Discussion

Basipetal conduit widening in tall trees

The convergence of $\beta \geq 0.20$ across a diverse array of woody plants that now includes some of Earth's tallest trees indicates a functional relationship between conduit diameter and height that minimizes the accumulation of hydraulic resistance (r) with height growth, independent of size, age, and climate (West et al. 1999; Anfodillo et al. 2006, 2013; Olson et al. 2014, 2018). Comparing conduit diameters at 1 cm from the tree tops (D_{h-top}) with those at tree bases (D_{h-base}) yielded a tenfold increase, substantially larger than predicted by MST, in which a factor of three is expected for

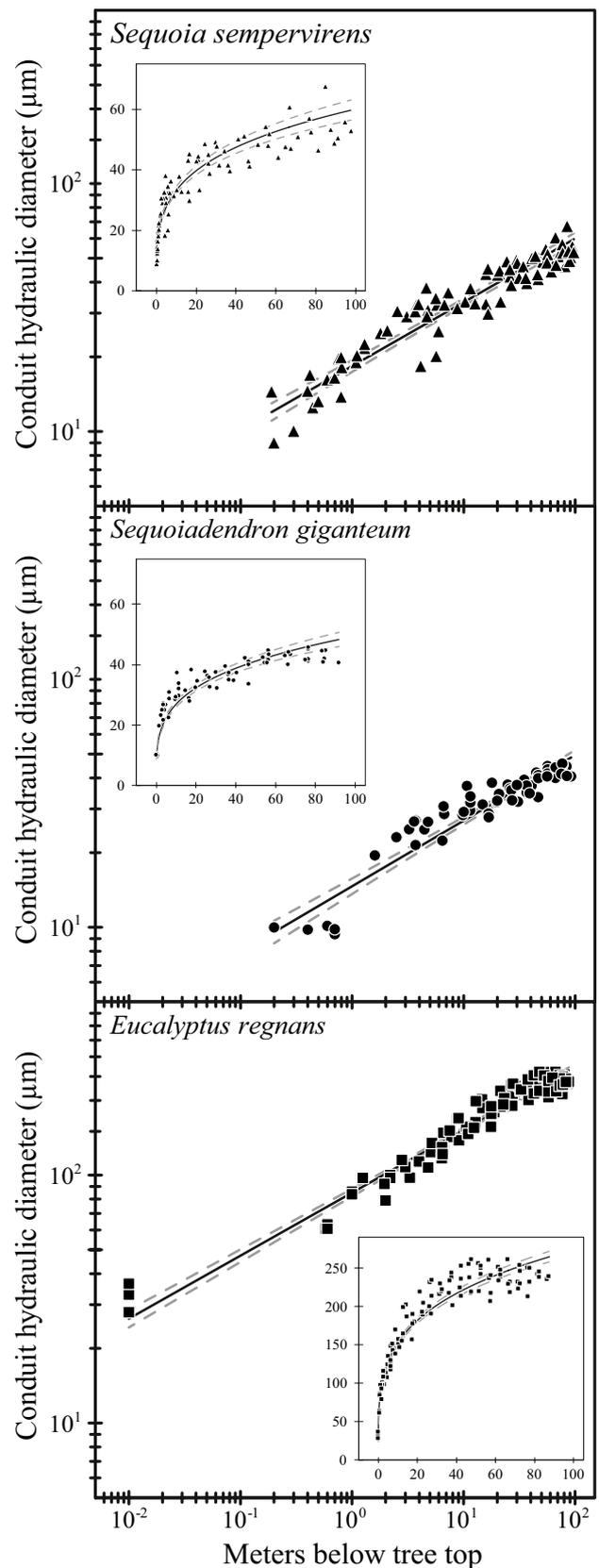


Table 2 Summary statistics for scaling relationships between tracheid or vessel hydraulically weighted diameter and distance from tree top for 15 tall *Sequoia sempervirens*, *Sequoiadendron giganteum*, and *Eucalyptus regnans* trees. The relationships were derived via reduced major axis regression. The scaling coefficient (α) is the intercept and the scaling exponent (β) is the slope of a power function taking the form $Y = \alpha X^\beta$

Name	# points	R^2	Intercept (μm)		Slope	
			α	95% CI	β	95% CI
SESE 1	23	0.96	5.36	4.49–6.40	0.27	0.25–0.30
SESE 2	18	0.83	7.12	4.90–10.34	0.23	0.18–0.29
SESE 3	17	0.93	6.70	5.26–8.54	0.23	0.19–0.26
SESE 4	20	0.90	4.73	3.51–6.37	0.27	0.23–0.32
All <i>Sequoia sempervirens</i>	78	0.90	5.62	4.92–6.43	0.26	0.24–0.28
SEGI 1	15	0.91	3.59	2.46–5.25	0.29	0.24–0.34
SEGI 2	10	0.89	3.65	1.99–6.70	0.29	0.22–0.37
SEGI 3	9	0.98	5.09	4.10–6.33	0.24	0.21–0.27
SEGI 4	10	0.87	8.79	5.84–13.22	0.18	0.13–0.24
SEGI 5	12	0.86	4.00	2.31–6.95	0.28	0.21–0.36
SEGI 6	11	0.81	6.47	3.71–11.29	0.21	0.15–0.29
All <i>Sequoiadendron giganteum</i>	67	0.89	4.33	3.66–5.12	0.26	0.24–0.29
EURE 1	22	0.98	24.90	21.61–28.70	0.26	0.24–0.28
EURE 2	23	0.97	30.09	26.20–34.55	0.24	0.22–0.26
EURE 3	19	0.92	26.25	19.71–34.98	0.25	0.22–0.29
EURE 4	22	0.94	19.22	15.05–24.54	0.29	0.26–0.33
EURE 5	22	0.95	29.01	23.98–35.10	0.24	0.22–0.27
All <i>Eucalyptus regnans</i>	108	0.95	26.35	24.29–28.58	0.25	0.24–0.26

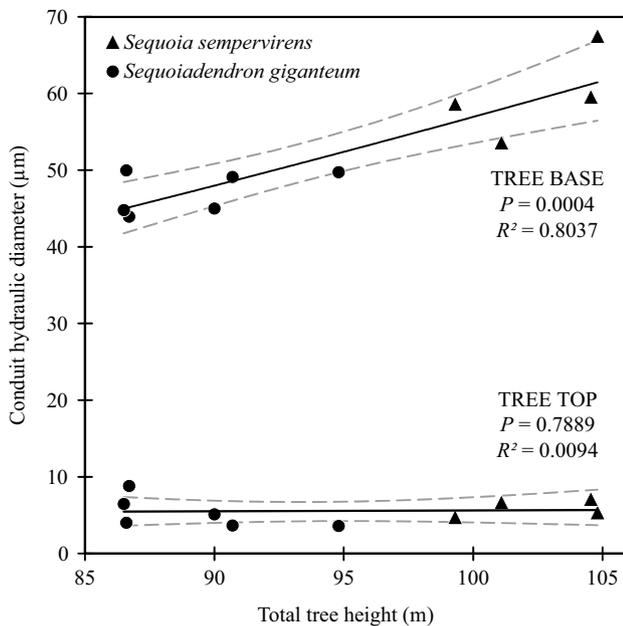


Fig. 2 Relationships between tree top or tree base tracheid diameter and total tree height for *Sequoia sempervirens* and *Sequoiadendron giganteum* combined. Dashed envelopes represent 95% confidence intervals. P -values refer to significance of slope. Relationships were derived via ordinary least squares regression on \log_{10} -transformed data

a 100-m tall tree (West et al. 1999; Anfodillo et al. 2006). This discrepancy was caused by an unrealistic number of about 18 branching levels that was assumed for a 100-m

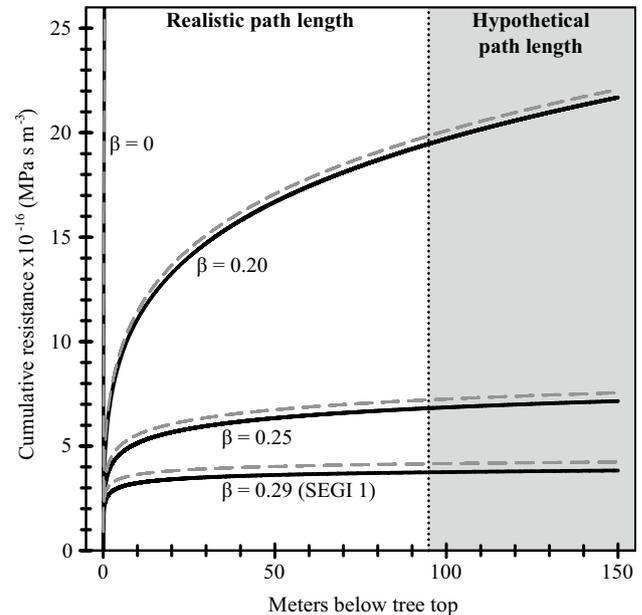


Fig. 3 Cumulative resistance as a function of distance from treetop, modeled for four different rates of basipetal conduit widening (β). Resistance was calculated via the Hagen–Poiseuille equation using the estimates for tree top tracheid size of one *Sequoiadendron*. Solid lines include estimates of axial variation in tracheid length, whereas dashed lines represent a constant tracheid length of 1.0 cm

tree by West et al. (1999) and shows that variation in conduit size is actually much higher. Moreover, including the entire hydraulic pathway from the roots where conduit diameters are largest (Domec et al. 2009; Petit et al. 2009; Jacobsen

et al. 2018a) through the distal-most leaf veins where they are smallest (Zwieniecki et al. 2002) should lead to relative increases even larger than a factor of 10, and consequently more than a 100-fold increase in lumen area. Although we did not measure variation in the number of conduits with height, some of the higher β values we observed may be associated with furcation, since β and furcation are expected to positively co-vary in vascular systems optimized for net carbon gain and hydraulic efficiency and safety (Hölttä et al. 2011). If true, this hydraulic architecture would represent a further departure from MST which assumes no furcation (West et al. 1999), and could yield even lower resistance and construction costs basipetally since a smaller number of wide conduits has lower resistance and less wall material than a larger number of narrower conduits, for a given xylem cross-sectional area (Tyree & Zimmermann 2002). Considering the Hagen–Poiseuille equation, such a dramatic increase in conduit width explains why r is negligible in the basal compared to the distal portion of the hydraulic pathway (Petit et al. 2010) as demonstrated by the steep and nonlinear decrease in water potentials distally along the flow path of some trees (Tyree and Zimmermann 2002).

Constraints on conduit widths

The degree of basipetal conduit widening depends on the sizes of apical and basal conduits. Angiosperm vessels at both positions typically widen with H , but those at the apex widen at a slower rate (Olson et al. 2014, 2018). Since the vast majority of r is concentrated near the tree tops where the conduits are narrowest (Petit et al. 2010), increasing D_{h-top} by just a few micrometers would substantially improve axial hydraulic efficiency. In *Eucalyptus regnans*, the wider D_{h-top} we observed in taller individuals did not compromise β , suggesting improved hydraulic efficiency over longer transport paths consistent with other angiosperms (Olson et al. 2014, 2018). In the conifers, however, the constant D_{h-top} with H we observed suggests that variation in the width of tree top tracheids may be constrained, perhaps due to excessive r through the small pits (Domec et al. 2008; Lazzarin et al. 2016) or low turgor pressures that limit cell expansion (Woodruff et al. 2004). Despite this apparent limitation in tree top tracheid width, β remained high in the conifers. Therefore, our results for D_{h-top} provide no evidence for constraints to β .

Constraints to conduit widths were more obvious at tree bases. D_{h-base} increased with H across the conifers, which we interpret as a mechanism allowing the maintenance of high β within individual trees as they grow taller. While this trend was observed only for the combined *Sequoia* and *Sequoiadendron* data, our interpretation is supported by the fact that D_{h-top} was not different between the two species and that they are closely related sister taxa (Farjon 2005). This trend

supports the notion of H driving variation in conduit diameter (Olson et al. 2014, 2018), but a closer look at the data also suggests that diameter may be limited. An upper limit to D_{h-base} was evident for all three species in our untransformed plots of D_h and L (Fig. 1), where beginning approximately 60 m from the tree tops, the rate of basipetal conduit widening decelerated below the power function as D_h approached an asymptote well above the tree bases. The apparent contradiction between these asymptotes in our untransformed plots of D_h and L , and increasing D_{h-base} with H in the conifers (Fig. 2) can be explained by height growth potential within a hydraulic limitation framework. That is, the *Sequoia* trees we sampled had a larger D_{h-base} and appeared further from an asymptote, whereas *Sequoiadendron* had a smaller D_{h-base} and appeared closer to an asymptote, suggesting less accumulation of r with additional height growth in *Sequoia* compared to *Sequoiadendron*. Indeed, the *Sequoia* we sampled were further from the greatest known height of 116 m for this species, whereas the *Sequoiadendron* were closer to the 96-m record (Sillett et al. 2015b). Thus, we predict the positive slope in the relationship between D_{h-base} and H (Fig. 2) would steepen to the left and flatten to the right with the inclusion of shorter and taller individuals, respectively, of these two species. Radial increases in tracheid and vessel diameters that approach a maximum in outermost annual rings at tree bases support this interpretation (Spicer and Gartner 2001; Leal et al. 2007).

That conduit width approaches an asymptote well above the tree base may imply constraints imposed by trade-offs that balance hydraulic efficiency against mechanical support, risk of freeze–thaw embolism, or the amount of fluid volume in the system. Withstanding the mechanical stresses imposed by gravity and wind should promote a higher ratio of wall investment to lumen area, typically achieved by adjusting lumen area rather than wall thickness, at the expense of hydraulic efficiency (Pittermann et al. 2006a; Sperry et al. 2008). Widening lumens toward a tree’s base would, therefore, compromise mechanical strength via an increasing ratio of lumen area to wall thickness. Larger diameter lumens would also be more prone to freezing-induced embolisms that expand upon thawing (Pittermann and Sperry 2003; Mayr and Sperry 2010), although this is an unlikely constraint for *Sequoia* or *Eucalyptus regnans* because these species rarely experience freezing temperatures. Wider conduits at the tree base would also significantly increase the volume of fluid (xylem sap) in the system, which has been suggested to undermine the efficiency of distribution networks (Banavar et al. 1999). Moreover, the vast majority of r is distributed toward the tree top while tree base conduits contribute very little to whole-tree hydraulic resistance (Fig. 3), so widening tree base conduits minimally benefits axial hydraulic efficiency. Therefore, the optimal balance between hydraulic efficiency and mechanical strength or volume of

water is most likely to constrain tree base conduit diameters and determine the degree to which basipetal conduit widening serves as a hydraulic compensation mechanism.

Distribution of hydraulic resistance

The distribution of axial r in *Sequoiadendron* that included estimates for changes in T_l with H is similar in shape to that using a fixed 1.0 cm T_l , but shows a systematic reduction in axial hydraulic resistance basipetally (Fig. 3). Acropetally, shorter conduits had almost no effect on r , suggesting that having shorter tree top conduits may be more important for hydraulic safety than efficiency. Given that tree tops experience the lowest water potentials (Tobiessen et al. 1971; Koch et al. 2004; Burgess and Dawson 2007; Williams et al. 2017) and are less buffered by hydraulic capacitance due to smaller stem volumes and higher cavitation resistance (Scholz et al. 2012), we suspect that short and narrow conduits at the tree tops confer hydraulic safety because narrower conduits are less prone to cavitation (Hargrave et al. 1994; Pittermann and Sperry 2006; Cai and Tyree 2010; Hölttä et al. 2011; Brodribb et al. 2016; Jacobsen et al. 2018b; Olson et al. 2018) and because narrower and shorter conduits that do cavitate will compartmentalize the embolisms to a smaller proportion of the hydraulic pathway (Comstock and Sperry 2000). Whereas variation in conduit length imparted a larger, but overall minimal, effect on r basipetally, conduit diameter and β were far more important. As described elsewhere (Becker et al. 2000; Petit et al. 2010), a high proportion of r was distributed in the top few meters of the tree where the conduits were narrowest (Fig. 3). In trees with larger β , hypothetically extending the hydraulic pathway basipetally (e.g., to include roots) suggests that small changes in conduit diameter there would impart a negligible hydraulic effect. Thus, the aforementioned notion that higher hydraulic efficiency trades off with lower mechanical strength, higher resistance to freeze–thaw embolisms, or larger volume of water may increasingly favor constraints on β toward tree bases where slight increases in conduit diameter offer minimal hydraulic benefits. Clearly, the distribution of hydraulic resistance is influenced by variation in conduit diameter and length along the entire flow path, but toward the tree top conduit diameters increasingly control whole-tree hydraulic efficiency.

Anatomical model for tree height growth

Building on well-known changes in wood anatomy that occur as trees enlarge (e.g., Panshin and Zeeuw 1980), we assemble the following model for the development of xylem conduit architecture that explains how individual conifers grow in height while minimizing the accumulation of r through the hydraulic pathway (Fig. 4). As each new annual

ring is produced, tree top tracheids are similar in diameter and length to the previous year's tree top annual ring, regardless of height growth— D_{h-top} varies little throughout a conifer's life. Conversely, tree base conduits are incrementally wider and longer with the addition of each new annual ring— D_{h-base} increases as the tree grows taller thus maintaining large β to minimize the accumulation of hydraulic resistance and compensate for the added path length. Along the trunk between the tree top and base, each new annual ring is composed of conduit widths and lengths according to β . This pattern continues throughout height growth until a limit to D_{h-base} is eventually reached due to trade-offs that constrain the ability to maintain β (Fig. 4). Note that this model is slightly different for angiosperms, whose tree top vessels are known to widen rather than maintain constant diameter with tree height growth (Olson et al. 2014, 2018).

Consistent with this model, basipetal conduit widening appears to be a universal trait among woody plants, regardless of size, age, habitat, or taxonomic affiliation (Anfodillo et al. 2006; Coomes et al. 2007; Petit et al. 2008, 2009, 2010, 2011; Bettiati et al. 2012; Olson et al. 2018). At the tops of the conifers, we found that D_{h-top} did not change across a range of H . At tree bases, radial increases in the diameters of conduits from older to younger annual rings agree with the model (Spicer and Gartner 2001; Leal et al. 2007). And since T_l changes in tandem with conduit diameter to maintain constant proportionality through pits versus lumens (Lancashire and Ennos 2002; Choat et al. 2008; Lazzarin et al. 2016), T_l is also predicted to increase radially within trees from older to younger annual rings and has been reported for *Sequoiadendron* trunk bases (Cockrell et al. 1971). Concomitant with increases in D_{h-base} with tree age is a rise in hydraulic conductivity (Pothier et al. 1989; Coyea and Margolis 1992; England and Attiwill 2007), also consistent with the model. While our evaluation of r for SEGI 1 suggests that even a slight widening of tree base conduits could continue to minimize the accumulation of r with height growth, our results suggest there is a limit to the widening. The axial profile of D_h formed a plateau in the basal portion of our study trees (Fig. 1), a trend also documented in other studies (Becker et al. 2003; James et al. 2003; Anfodillo et al. 2006; Petit et al. 2010), that may be symptomatic of a ceiling to D_{h-base} due to trade-offs imposed by the need for mechanical support, the reduced risk of freeze–thaw embolism, or the minimization of fluid volume in the distribution network.

Conclusions

Across a wide array of woody plants, now including some of Earth's tallest trees, the rate of basipetal conduit widening is consistent with minimizing the accumulation of hydraulic resistance with height growth. Despite the wider basal

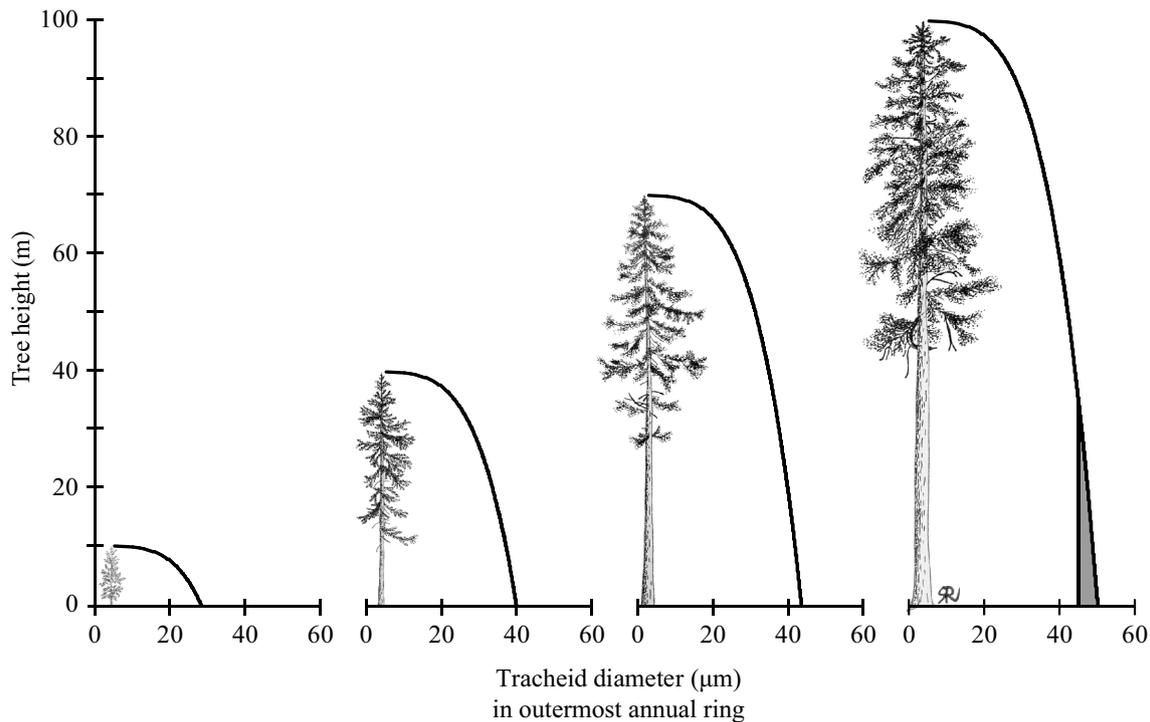


Fig. 4 Graphical model of axial variation in tracheid diameter in a conifer's main trunk as height growth occurs. Each of the four panels represents a snapshot in time when the tree's total height is 10, 40, 70, or 100 m. Each curve shows the axial profile of average conduit diameters in the outermost annual ring. The shaded region of the curve for the 100-m tree represents tracheid diameters that approach a maximum width. Tree top conduit diameter (D_{h-top}) and the rate

of basipetal conduit widening (β) remain constant throughout height growth, while tree base conduit diameter (D_{h-base}) widens among newer annual rings until the maximum conduit width is reached. In this example, $D_{h-top} = 5 \mu\text{m}$ and $\beta = 0.25$; $D_{h-base} = 50 \mu\text{m}$ in the absence of constraints on maximum conduit width. Tree drawings by Rikke Reese Næsborg, used with permission

tracheid diameters we observed in taller trees, however, the power function typically applied to describe the vertical profile of conduit diameters overestimated the size of conduits in the basal portion of the study trees, indicating a constraint on the rate of basipetal conduit widening. The distribution of axial hydraulic resistance suggests that conduit length is relatively unimportant compared to width and that widening conduits at the tree base offers minimal hydraulic benefit that may consequently trade off with other factors that promote smaller diameter conduits. Our graphical model describing radial and axial changes in xylem anatomy during tree enlargement summarizes many anatomical and physiological trends observed in tree wood.

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