

Scaling of Xylem Vessel Diameter with Plant Size: Causes, Predictions, and Outstanding Questions

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Abstract

Purpose of Review This review shows that a more or less constant rate of tip-to-base vessel widening across species, together with the assumption that wider vessels are more vulnerable to embolism, suggests how climate should limit maximum vegetation height; together, these two factors predict a maximum mean vessel diameter permitted by temperature and water availability at a site and thus maximum plant height.

Recent Findings Empirical work makes it increasingly clear that the main driver of variation in mean vessel diameter is plant size, specifically the length of the conductive stream. Anatomical evidence, together with hydraulic optimality models, suggests that this vessel diameter-stem length relationship is the result of natural selection favoring the maintenance of constant hydraulic resistance over size increases. From their very narrow termini, vessels widen predictably from the stem tip to the base, following approximately a power law, i.e., with very rapid widening toward the tips and nearly constant diameter toward the base. This size

dependence must be taken into account when studying the hydraulics-climate relationship.

Summary This review discusses outstanding predictions that require testing, including the following: variation in the vessel diameter-stem length relationship should involve factors such as vessel length distributions, pit characteristics, leaf area, and wood density; leaves higher in trees should have higher terminal leaf vein-petiole base vessel widening rates; species without “disposable” units (e.g., columnar cacti) might have different widening rates; and within-plant widening rate should vary as plants approach their height limits. Finally, we emphasize the need to standardize for size in making comparisons of vessel diameter variation.

Keywords Allometry · Vessel diameter · Plant height · Ecological wood anatomy · Xylem anatomy · Xylem embolism

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Introduction

Students of plant hydraulics are confronted with a striking empirical pattern: sample at a random sufficient range of plant sizes and stem size predicts conduit diameter (Fig. 1). In explaining this pattern, three questions require addressing in order. The first is whether this pattern is real or just sampling error. Spanning a range of plant size from less than a meter tall to nearly 100 m and emerging worldwide across all major plant lineages and plant habits, it is clear that the pattern represents biological reality and is not simply the result of improper sampling [1, 2, 3, 4, 5•, 6]. The second question is what biological process causes this predictable scaling with size, and why does the conduit diameter-stem length slope, when correcting for tip vessel diameter, converge in large samples on 0.2? Finally, what factors can account for the residual variation about the scaling slope?

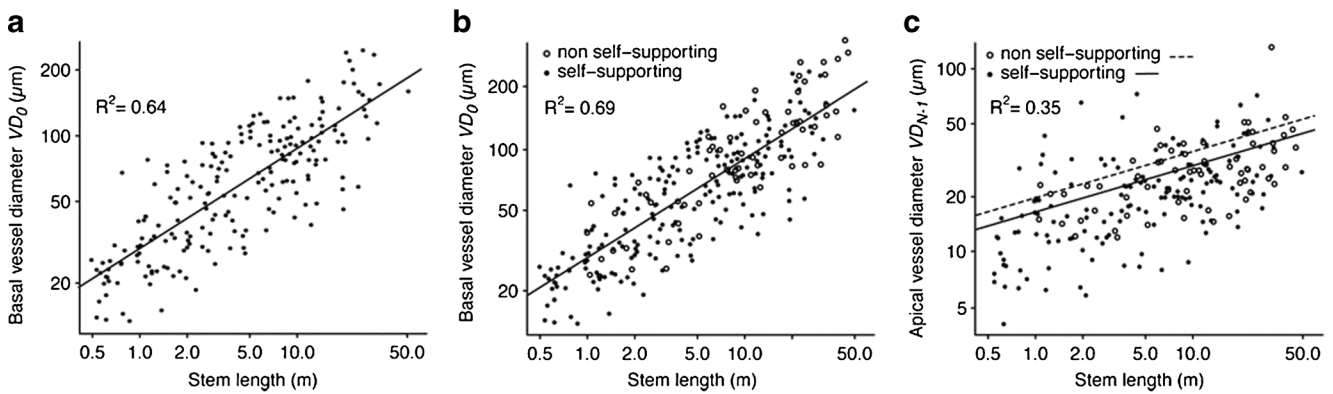


Fig. 1 Scaling of vessel diameter (VD) with stem length (SL) across angiosperm species and habits. Points are species mean values. **a** Basal vessel diameter (VD_0) scales predictably with SL across self-supporting angiosperms. **b** Basal vessel diameter (VD_0) scales similarly with SL between self- and non-self-supporting species. **c** Twig apical vessel diameter (VD_{N-1}) scales with SL across self- and non self-supporting

species, meaning that taller plants and longer lianas have predictably wider vessels not only at the stem base but also at the stem apex. $N = 209$ species in **a**, 275 in **b**, and 215 in **c**. Regression models predicting VD_0 and VD_{N-1} based on SL and habit (not shown) show that vessel diameter scales with $SL^{0.47}/SL^{0.24} = SL^{0.23}$. The scaling exponent is very close to the 0.2 predicted by models

In this review, we suggest that the first two questions have been satisfactorily answered and that the general pattern is the result of natural selection favoring the maintenance of constant hydraulic resistance over increases in plant size. As to the third question, in log-log plots, there is an order of magnitude of relative variation about the Y axis that requires explanation. It is here where questions regarding the influence of factors such as climate, habit, conduit length, pit characteristics, and growth ring types, via their potential effects on Y -intercept, need addressing. The sequence of questions—is the pattern real or error, what causes the pattern, and what explains the residual variation?—provides the framework for addressing questions such as the effect of growth rings, conduit length distributions, or climate. In this review, we first treat the question of the cause of the general pattern, selection shaping resistance with size increase. We then treat some of what is known and some of the open questions regarding the causes of the residual variation about the Y axis, including climate and growth rings. We also discuss methodological considerations derived from vessel diameter scaling with plant size for physiological and anatomical studies.

Having the key role of transporting water from the roots to the leaves in angiosperms, xylem conduits play a crucial physiological and ecological role. Vessels in angiosperms are formed by the superposition of vessel elements to form continuous conduits [7]. In contrast with gymnosperm wood, in which the water-conducting cells, known as tracheids, both conduct and provide mechanical support [8], vessel elements in angiosperms leave mechanical support mainly to imperforate tracheary elements, usually libriform fibers, less commonly tracheids or fiber-tracheids [7]. This differentiation of cell function has been suggested as helping the angiosperms to be able to diversify into so many different environments and habits [9, 10]. Because they have been studied in greater

detail, our discussion here focuses mostly on angiosperm vessels but applies to tracheid-bearing plants as well.

The rate of water flow along a stem segment depends on many factors, but vessel diameter has been traditionally discussed as the factor largely defining the efficiency of water transport and thus the rate of water use in a tree [11]. However, the importance of vessel diameter in explaining the efficiency of water transport is often discussed without taking into account that vessels change in diameter along stems. Ranges of variation in vessel diameter at the base of angiosperm stems can go from a few micrometers in very short woody species, to nearly a millimeter in diameter in very long lianas [6]. As will be explained here, wider vessels at the bases of longer stems compensate for the increase in resistance to water flow caused by the increase in plant height or length. As a result, instead of being mainly the result of vessel diameter at the base or at breast height, the efficiency of water use by a plant is largely determined by the resistance of the whole conductive path along the stem.

The Reality of the Pattern: Variation in Vessel Diameter with Plant Size

Changes in vessel diameter with plant size have been documented for centuries. In his 1675 book *Anatome Plantarum*, Malpighi M [12] noted that there is a radial increase in vessel diameter in trees (Fig. 2) and that “the widest vessels (“trachearum”) are found in the most recent annual ring” (Fig. VIII 36, p. 19). A few years later, in his book *Anatomy of Plants* [13], Nehemiah Grew also described this pattern, noting that “for the most part, the *Aer-Vessels* are somewhat, more or less, amplified in every new *Annual Ring*” (p. 131). Two hundred years after Grew’s observations, Sanio described tracheids becoming progressively wider from the pith to the cambium and from the branch tips to

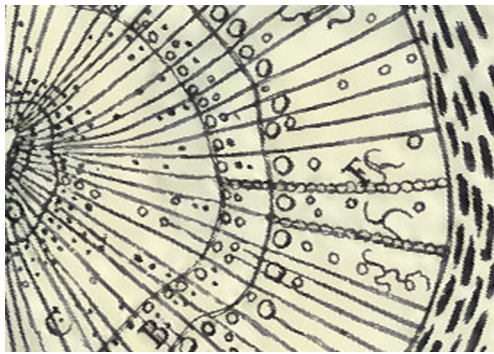


Fig. 2 Radial increase in vessel diameter in the growth rings of a young oak stem from Malpighi 1675, who states that “the widest vessels (“trachearum”) are found in the most recent annual ring” (Fig. VIII 36, p. 19) [12]. Vessels increase in diameter radially because successive growth rings are associated with taller plants, longer conductive path lengths, and thus wider vessels (image from the Biodiversity Heritage Library; digitized by the University of Toronto. www.biodiversitylibrary.org)

the trunk base [14]. Although originally described for gymnosperm tracheids, these patterns were also observed in angiosperm vessels and became known as Sanio’s laws [15]. Since Sanio, the covariation of vessel and plant size has often been acknowledged in comparative and ecological wood anatomy [16–21]. Vessel diameter has been shown to be associated with plant habit, with wider vessels being more common in trees and narrower vessels in shrubs [22, 23]. In most cases, this vessel size-plant size association has been discussed separately from ecological trends such as the tendency for vessels to be on average wider in moister communities [24], though some have discussed their interrelation. For example, Carlquist S [25] noted correlations between vessel size and climate and between tracheid size and plant size, in *Tasmannia*. He noted that climate correlations are “overlain” on size correlations, with wider tracheids in warmer and moister locales, but a convincing mechanism for why conduits should be predictably wider in larger plants was still lacking.

While recent anatomists have focused on vessel diameter variation across species mostly with respect to climate correlation, physiologists have explored vessel size differences through hydraulic models. Table 1 gives examples of key aspects of representative models to give an idea of their coincidences and differences. From their outset, these models have included fluid mechanics as a central consideration to describe plant conductive systems [recent examples include 26, 27–32, 33••, 34••, 35]. These models all share their inclusion of Poiseuille’s law as a central consideration. This law states that flow through a tube is directly proportional to the pressure and to the fourth power of the radius of the tube and inversely proportional to the length of the tube and to the viscosity of the liquid [36]. Vessel diameter is thus a central variable in these models. These models, as part of the tradition of plant physiology, grew in tandem with significant advances in the laboratory study of xylem hydraulic, and the development of the tension-cohesion theory [37–39]. We now turn to the

Table 1 Aspects of selected hydraulic optimality models with respect to tip-to-base conduit widening and related variables

Model	Conduits widen tip to base	Vessel diameter-stem length scaling (i.e., widening rate)	Tree hydraulic resistance with ontogeny	Internal branching network (conduit) area, base to tip	External branching network (stem) area, base to tip	Conduit furcation	Conduit density, base to tip	Sap velocity, base to tip)
Shinozaki’s pipe model [40, 41]	No	–	Increases	Area preserving	Area preserving	No	Constant	Constant
WBE model [26]	Yes	0.25	Constant	Area decreasing	Area preserving	No	Constant	Increases
WBE + Anfodillo [2]	Yes	About 0.20	Constant	Area decreasing	Area decreasing	No	Increases	Increases
Hölttä [34••]	Yes	0.17, but variable according to furcation	Increases slightly	Area preserving (approx.)	Area decreasing mechanical aspects not considered	Yes	Increases	Approx. constant (not reported)
Savage et al. [33••]	Yes	0.5	Constant	Area preserving	Area preserving	Yes	Increases	Constant
Murray’s law [29]	Yes	Variable, inversely related to furcation	Not predicted	Area increasing	Area decreasing mechanical aspects not considered	Yes	Increases	Decreases

details of some of these models to explore the main adaptive hypothesis explaining the pervasive pattern of vessel tip-to-base widening across the woody plants.

Why Vessel Diameter Scales with Plant Size

A crucial distinction between hydraulic models is whether or not they include tip-to-base (basipetal) conduit widening (“taper”). Among the hydraulic models with non-tapered conduits, a seminal one was the pipe model [40]. In this model, a 1:1 relationship between leaf and conduit (pipe) number was proposed [41]. Conduits in models based on the pipe model are conceived of as cylinders and thus have a constant diameter along the stem [42]. Decades after the pipe model, West GB et al. [26] proposed an optimality model (West, Brown, and Enquist (WBE) model hereafter) describing hydraulic networks in plants in which vessels widen from the stem tips toward the base of the trunk and form a fractal-like supply network. Although this widening had been implicitly recognized centuries earlier, the WBE model was the first to postulate why and how this widening occurs [43].

Vessel widening from the leaves to the stem base can be explained using basic hydraulic principles. The terminal vessels in leaves are narrow because selection favors high surface area, maximizing diffusion of water out of vessels. Vessels widen toward the base, a pattern that can be explained by Poiseuille’s law showing that the resistance in a pipe accumulates linearly as the pipe lengthens, all else being equal [36]. This means that flow decreases predictably with each length increment added of uniform diameter pipe. Poiseuille’s law also shows that very small increases in pipe diameter produce dramatic increases in flow, increasing with radius to the fourth power in ideal capillaries [44]. Maintaining resistance more or less constant, thus ensuring that all terminal elements of the system receive the required water, demands that conduits widen tip to base (Fig. 3) [26].

The minimum rate at which this widening should occur is predicted by hydraulic optimality models based on WBE [42]. This minimum rate can be estimated by assuming that hydraulic resistance in a vessel is maintained constant along the stem [2], even as a tree grows from a tiny seedling to a forest giant. Different rates of vessel widening, expressed by the scaling exponent b , are presumably possible developmentally. Figure 4 shows different possible rates and how they would determine different values of total hydraulic resistance in a single pipe relative to the resistance of the apical portion of the vessel (R_{TOTAL}/R_{APEX}) using Poiseuille’s law assumptions [5•]. Different values of b would lead to different rates of change in resistance with pipe length. For a rate of about 0.2, hydraulic resistance remains more or less constant with increasing stem length (see bold line in Fig. 4). For values of b lower than 0.2, vessels widen more slowly and the resistance increases (see discontinuous lines in Fig. 4) as plants grow

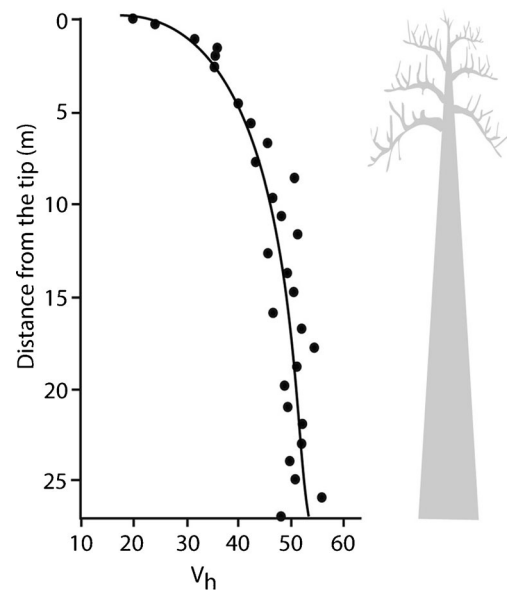


Fig. 3 Variation in tracheid diameter (hydraulically weighted, V_h) in the last tree ring at different distances from the tip of the tree in *Larix decidua*. Conduit diameter widens toward the base of the tree, changing very quickly near the tip and very slowly near the base. Selection might favor concentration of resistance in terminal regions with high turnover, permitting continuous adjustment of whole-tree resistance. Empirical studies must sample carefully with the form of vessel widening rates in mind. After Anfodillo T et al. [2]

taller. Increase in resistance implies diminishing flow rates and thus drops in photosynthetic productivity with height [42]. If productivity dropped with height increase, then tall plants would be at a selective disadvantage [45].

At the other extreme, values far above 0.2 would lead to stems with very wide vessels that, while not increasing resistance along the stem (see dotted line in Fig. 4), might also lead to lowered productivity, for two potential reasons. One is that, as we will explore in more detail in the next section, wider vessels seem to be more vulnerable to the formation of gas embolisms. Water is drawn up through the xylem under negative pressure, so the introduction of an air bubble into the conductive stream, or the vaporization of water, leads to the expansion of the gas until pressure equilibrium is reached. This gas embolizes the vessel, meaning that it cannot conduct water. Some models [e.g., 33] suggest that beyond a certain widening rate, the gain in conductive rate is low relative to the increase in vulnerability to embolism. From the point of view of natural selection, increases substantially beyond this point appear to be invitations to embolism that provide little benefit in terms of carbon capture. The other reason [e.g., 46] is that excessive fluid volumes could be selected against, presumably because of the metabolic cost of producing and maintaining long and wide vessels and any associated respiring tissue [47]. Whatever the exact cause, as with excessively narrow vessels, excessively wide ones are presumably associated with lower growth rates and absolute reproductive investment.

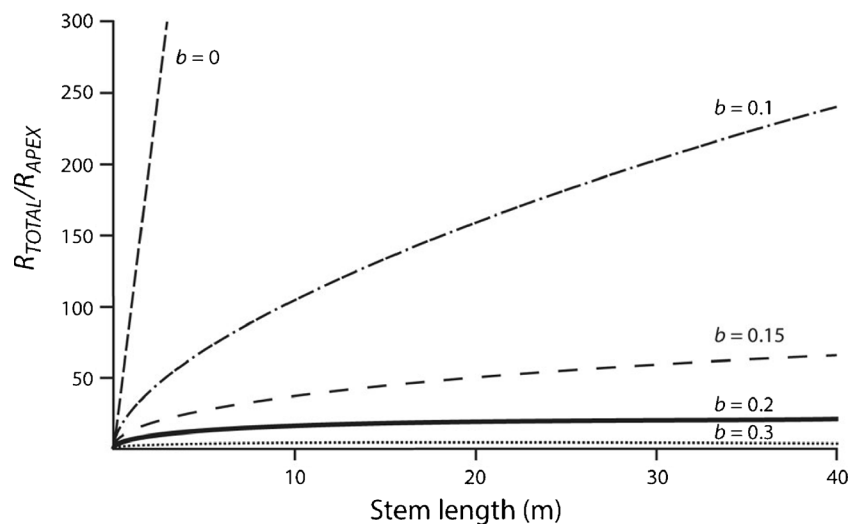


Fig. 4 Vessel widening rate and hydraulic resistance with stem length. Following Poiseuille's law, vessel widening rate (b) determines the value of relative hydraulic resistance (total resistance/resistance of the apical most vessel (R_{TOT}/R_{APEX})) in a series. For values of $b < 0.2$, vessels widen slowly from tip to base and hydraulic resistance increases with increasing stem length. The lower the value of b , the slower the rate of widening and the faster resistance increases with stem length. For values

$b > 0.2$, vessels widen very quickly to the base, and while hydraulic resistance remains constant with stem length, the amount of fluid relative to leaf area is large and there is a higher risk of embolism. Values of $b = 0.2$ or slightly above lead to practically constant hydraulic resistance with stem length and to maximally safe and efficient conductive systems. After Olson ME et al. [5••]

The predicted widening of vessels can be described by the expression $VD \propto SL^{0.2}$, which means that conduit diameter (VD) should be proportional to stem length (SL), with the power being the “widening exponent,” describing how fast or slow conduits widen from the stem tip per unit stem length. Conduit diameter-stem length exponents < 0.2 (slow widening = high hydraulic resistance) or well above 0.2 (rapid widening = risk of breakage of the conductive stream) will tend to be selected against, leading to convergence on the 0.2 exponent or slightly above [42], regardless of phylogenetic affinity, habit, or climate. This theoretical prediction is being borne out to a remarkable degree by empirical work.

Empirical Data Coincide with Optimality Predictions of Widening Rate

The predicted vessel widening rate from hydraulic optimality models coincides remarkably with empirical data. Widening rates at or close to 0.2 have been observed both when studying vessel diameter increase along stems of individuals [48–50] and also across species, continents, and habitats [5••]. These observations have been based on sampling stretching across the 50 or so orders or major clades of flowering plants, coming from a very wide of habitats including freezing-prone temperate highland forests to tropical lowland forests, mangroves, temperate forest and shrubland, deserts, etc. (Fig. 1a) [5]. The coincidence of widening rate between empirical data and theoretical models goes beyond angiosperms, having been observed in the tracheids of conifers [2–4, 5••, 6–32, 33••, 34••, 35–41, 42••, 43–51]. When only the conduit

diameter at the stem base in interindividual or interspecific scaling is measured, the exponent measured is usually in the range of 0.4–0.5. This is because conduit diameter at the stem tip also increases with height [5••], and therefore, the scaling of the conduit at the base appears larger than expected. There are two approaches for correcting for apical vessel diameter widening [2, 5••]. When measuring only basal conduits, scaling with stem diameter (SD) will be around 0.3 (i.e., $D_h \propto SL^{0.5}$ and $SL \propto SD^{0.67}$, then $D_h \propto SD^{0.33}$), also congruent with the exponents observed [52, 53].

If basipetal vessel widening is the product of natural selection favoring the maintenance of constant hydraulic resistance over size increases, then there is no reason to expect plants of different habits to depart markedly from this pattern, given that the properties of water are constant. Accordingly, the 0.2 widening rate emerges even when sampling across woody plant habits, including trees, shrubs, subshrubs, succulents, arborescent monocots, cacti, mangroves, parasites, bottle trees, etc. [5••]. Moreover, lianas, a habit that has been repeatedly highlighted for their remarkably wide vessels for a given SD, comply with the prediction. The very wide vessels of lianas have been explained by the need to supply a large canopy through a very narrow stem [54]. However, lianas have mean vessel diameters that would be expected given stem length (Fig. 1b) [6–32, 33••, 34••, 35–41, 42••, 43–55]. Thus, sampling across habits, clades, and biomes converges on an exponent of about 0.2 (Fig. 5).

The predicted vessel diameter-stem length relationship does not seem to show a phylogenetic effect. The tendency for closely related species to resemble one another more than

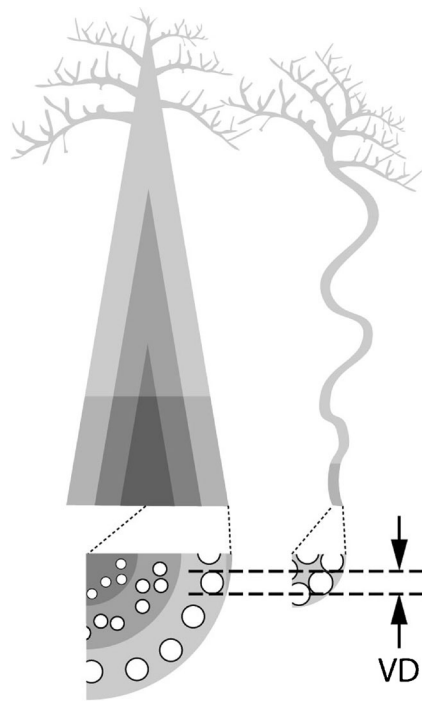


Fig. 5 Vessel diameter (VD) in self- and non-self-supporting plants. Center to periphery increases in vessel diameter with stem length in a tree. Each layer of xylem (*gray cones*) corresponds to successively older and taller stages of the stem's growth. Because vessels become wider basally with increasing stem length, vessels become wider to the outside of a tree. Despite its much narrower stem diameter, the liana has a similar vessel diameter to the tree, given that their stem lengths (and thus conductive path lengths) are similar as well

to distantly related species, a pattern known as phylogenetic effect or phylogenetic “inertia” [56], has been tested repeatedly with respect to the vessel diameter-stem length relationship [52, 53, 57]. In no case has any phylogenetic effect ever been detected, meaning the relationship is highly labile evolutionarily [58]. This is easy to observe by simple inspection, with countless clades having closely related species of vastly different sizes and therefore vessel diameters. For example, there are dozens of groups in which lianescent species are closely related to self-supporting ones, as between the lianescent *Trimenia moorei* and the self-supporting *Trimenia neocaledonica*. In this example, vessel diameter follows stem size very closely with the 18-m-long liana having vessels 93 μm wide and the 2.5-m tall tree having vessels 65 μm wide [5••]. This evolutionary lability means that stem length predicts vessel diameter, but phylogenetic relationship does not.

Moreover, pit characteristics seem likely to scale with conduit size such that pits do not represent hydraulic bottlenecks. If features such as pit aperture and chamber diameter, membrane permeability, or margo area remained constant from tip to base, then hydraulic resistance would likely increase as trees grow taller because of the increasingly small pit conductivity relative to vessel volume. Recent data from tracheids along the length of a tall giant sequoia [47] show that total

margo permeable area scales with conduit lumen area and thus tree size in a way that maintains the relative total margo permeability constant with respect to tracheid lumen area. This strongly suggests the action of natural selection on pit characteristics in the maintenance of total pit resistance constant compared to lumen resistance [as suggested by 8].

We are aware of no other plausible reason to explain the remarkable coincidence between data from nature and the predictions of optimality models that does not involve adaptation by natural selection. This coincidence is grounds to suspect that model assumptions are correct or at least are in the right direction and therefore suggests that it is essential to account for stem size when studying variation in vessel diameter across climates.

What Causes Variation About the Y Axis? The Role of Climate

There is abundant empirical evidence of the association of vessel diameter with both climate and also with plant size. The cornerstone observation of the field of ecological wood anatomy is that plants of dry and cold areas have narrower vessels, whereas plants of moist and warm places have wider vessels [16]. This global pattern has been explained by appealing to the greater embolism resistance of narrow vessels in situations of cold and drought [59]. At the same time, vessel diameter seems to reflect the length of the conductive path of water along stems. As a result, vessels of small shrubs or short statured trees have narrower vessels, whereas tall trees or long lianas have wider vessels [60]. These sets of associations pose the question of which, climate or size, is the main driver of variation in vessel size globally.

Climate seems to have a less important role than plant size in explaining vessel diameter variation. The role of climate can be examined taking into account the size of the plant when calculating the associations with vessel diameter. Once plant size is taken into account, the residual variation in vessel diameter is statistically significantly associated with climate variables, but this association is low [5••, 6–32, 33••, 34••, 35–41, 42••, 52]. For example, an index reflecting mean temperature explained 20% of the raw non-size standardized variation in vessel diameter. Once stem size was taken into account, this mean temperature index was only able to explain 6% of the variation in vessel diameter [5••]. In contrast, stem length explained 63% of total variation in vessel diameter [5••]. Results such as these show that, in comparison with climate, plant size is by far the main driver of variation in vessel diameter at a global scale.

That plants in moist environments tend to have wider vessels than plants in dry environments is a pattern known for decades [61], but the interpretation of this pattern needs to change in light of the causal relationship between plant size and vessel diameter. The tendency for average community

vessel diameter to be wider in moister areas [59] is due to the wider height variance in these communities. Plant minimum size is similar across communities, but maximum size is greater in warmer and moister areas [62]. Greater maximum size means greater community-wide size variance and, therefore, higher mean vessel diameter. Rainforests have on average wider vessels than deserts because rainforest plants are on average taller. Correcting for stem size, the mean vessel diameter of a plant from the rainforest will be similar to a similar-sized desert plant. This is why plant size must be incorporated into ideas regarding how climatic selection pressures shape vessel diameter across species and continents. Studies of the vessel-climate relation usually invoke a positive correlation between vessel diameter and cavitation vulnerability, and this assumption potentially plays a role in understanding the link between basipetal vessel widening and vegetation height.

Implications for Forest Management: Plant Height and Vulnerability

A variety of observations, both experimental and comparative, suggest that wider vessels are more vulnerable to drought-induced embolism than narrow ones [30, 63, 64, 65••, 66–69]. The mechanism of the increase in vulnerability seems to involve a combination of factors. First, pit area increases with vessel wall surface and thus diameter and so does the chance of a large membrane pore [64]. Pit membranes become deflected when an embolized vessel is adjacent to a functional one. The negative pressure in the functional vessel draws the membranes shared with the adjacent non-functional vessel toward its pit apertures [70]. This deflection distends the membrane, widening pit membrane pores and increasing the chance that large pores will become wide enough to allow the passage of gas from the embolized vessel into the functional one, a process known as air seeding [66]. Narrower vessels have lower absolute pit area, and so, selection plausibly favors narrow vessels in embolism-prone situations. The abundance of internal sculpture in vessels, particularly in drylands, suggests that adhesion to the vessel internal walls might also play a role in resisting cavitation. If this is the case, then the much greater wall area per unit water volume in narrow vessels would be involved in the greater difficulty of detachment of the water column from the wall [59].

There are numerous common phenomena that have never been explained without invoking a vessel diameter-embolism resistance relationship. For example, when growth rings are present, they universally proceed from wide vessels to narrow ones, in parallel with increasing seasonal drought or cold [7]. In any given site where plants with growth rings are present, they usually grow side by side with plants that do not have growth rings. As a result, it seems difficult to invoke temperature or drought-induced turgor drops as agents that cause plants passively to produce narrower vessels by virtue of shorter developmental time

due to cold or less cell expansion pressure due to drought. That latewood vessels are adaptively favored in end-of-season situations of drought or cold seems more likely. Moreover, there seems to be no plausible alternative explanation for the narrow vessels that so often accompany wide vessels of dryland plants and lianas [55, 59–64, 65••, 66–71] that does not involve their embolism resistance. A mechanical role for narrow liana vessels has been postulated [72], but these explanations give no plausible account of why in these situations, the usual “skeletal” imperforate tracheary elements (libriform fibers, fiber-tracheids, or true tracheids) should be replaced by vessel elements [55]. Instead, narrow plus wide vessels in lianas and dryland plants seem to have clear examples of situations in which selection favors wide, efficient conduction in wide vessels and safety in narrow ones [72]. Many other observations can be added. Why wide earlywood vessels are deactivated early while narrow latewood vessels conduct, sometimes for years, seems impossible to explain without appeal to an association between conduit width and vulnerability [e.g., 73]. Countless species have apparent safety features in latewood such as true tracheids, vasicentric tracheids, vascular tracheids, latewood scalariform perforation plates, and even internal vessel sculpture [74, 75]. When present in latewood and not in earlywood, these features are always associated with narrow vessels (or just preceded by narrow vessels in the case of vascular tracheids). The most economical way of explaining all of these observations is by appealing to the greater embolism resistance ability of narrow vessels.

Rejecting the diameter-vulnerability link requires an alternative explanation that explains all of these observations as well or better. The experimental evidence regarding the diameter-vulnerability link is at the moment regarded as weak [76]. However, as we discuss in the following, if vessel diameter scales with distance from the stem tip, it seems likely that to be comparable measurements of vulnerability must be standardized with reference to distance from the stem tip. Explanations must strive to account for all of the evidence, and at present, the vulnerability-diameter link would seem most parsimoniously to explain the observed data, including structural patterns. If true, then the diameter-vulnerability link in combination with the pervasive pattern of tip-to-base vessel widening leads to testable expectations regarding how plants should react both adaptively and ontogenetically to changes in climate.

A more or less universal rate of vessel widening with distance from the tip, in combination with the assumption that wider vessels are more vulnerable to embolism, leads to a prediction regarding the response of maximum vegetation height to climate change. Ontogenetic increase in tree height inevitably involves wider conduits basally, which are more vulnerable to breakage of the conductive stream. Via the diameter-vulnerability link, water availability and freezing regimes determine the maximum conduit diameter that is viable at a given site. Because vessel diameter and height are related, climate thereby determines maximum vegetation height.

Alterations to water or temperature regimes, as via anthropogenic climate change, should therefore produce predictable vegetation height responses. Because the bearers of the widest vessels in a community are necessarily the tallest plants, it is possible to anticipate die-offs of the largest trees under increasing drought, all else being equal. Early signs should be revealed as apical branch desiccation in the tallest trees with increases in vapor pressure deficits [77]. These predictions seem consistent with longstanding empirical observations that the largest plants are most vulnerable to drought-induced mortality [78–81]. That these individuals necessarily have the widest conduits in their communities would seem likely to be involved in this vulnerability. Observations of treeline plant height increase under global [82] or artificial [83] warming suggest that higher temperatures permit wider conductive cell sizes and therefore taller plants [see also 84]. Factors such as variation in rooting depth and pit characteristics must affect drought vulnerability, but in general, empirical data do seem consistent with our hypothesis.

This hypothesis is readily testable. It predicts that all else being equal (e.g., pit features), the basal xylem of taller individuals should be more vulnerable to embolism than in small ones. One way to keep other features relatively constant is to examine vulnerability along the lengths of stems or across closely related species. The hypothesis predicts that there should be a gradient of vulnerability in individuals from tip to base. Twigs from the tops of tall individuals should be more vulnerable to embolism than those of shorter conspecifics. It suggests that the plants with the relatively widest vessels and the shallowest rooting depths for their heights at a given site will be the most vulnerable to drought-induced mortality. It suggests that factors such as pit dimensions and membrane thickness could explain the residual variation in the vessel diameter-vulnerability-plant size relationship [e.g., 85]. This hypothesis is perhaps the most significant outstanding question suggested by the observation of a more or less constant rate of vessel widening across species. We detail several other important questions next.

Scaling of Vessel Diameter: Outstanding Issues

The pervasiveness of the relationship between vessel diameter and plant size has only been recently quantified. As a result, there are still many important issues to be addressed. We treat just some of these here.

But What About Ring Porous Species? Variation About the VD-SL Y Axis

The question “but what about ring porous species?” is the one most often asked with regard to patterns such as those in Fig. 1. Here, we unpack three different issues nested within this question. The first issue can be summarized as the assertion that “the

existence of variational phenomena, such as growth rings, invalidate the notion that vessel diameter is statistically predictable given stem length.” This assertion translates into the statement that the pattern in Fig. 1 is not biologically real and is simply the result of sampling error. But examining Fig. 1, it is very unlikely that the pattern recovered, spanning a tenfold range of stem length and with an $R^2 > 0.7$, is due to sampling error. The pattern emerges in all studies conducted that sample a sufficient range of stem sizes; our sampling includes ring-porous species plus most other growth ring types, trees, shrubs, herbs, lianas, succulents, parasites, mangroves, creepers, climbers, tree cacti, etc., from treeline to lowland temperate habitats to tropical dry forest, tropical rainforest, hot desert, cold desert, tropical savannah, and other habitats. Vessels were measured across growth rings and their diameters averaged. The pattern in Fig. 1a is the one that emerges. This means that the pattern is a biologically real one and one requiring explanation.

The second question is therefore “how are variational phenomena, such as growth rings including ring porosity, involved in the vessel diameter-stem length relationship?” Addressing this question will need to examine how the sources of potential variation in vessel diameter, such as climate, habit, vessel length, or growth rings, contribute to the variation about the Y axis in the vessel diameter-stem length relationship. This is the area in which most research is needed in understanding the vessel diameter-stem length relation. We present Fig. 1 on a log scale, because it is the relative variation in vessel diameter and stem size that is of biological interest. A difference in vessel diameter of 10 μm is of little significance to a plant 50 m tall, but of major significance to a plant 0.5 m tall; log transformation highlights such relative and biologically informative variation. A remarkable feature of Fig. 1 is that there is a more or less constant degree of relative variation in vessel diameter across the full range of stem lengths sampled. This makes it very likely that the variation about the Y axis, that is, of vessel diameters possible for a given stem length, is of biological significance and not all simply sampling error. We mentioned previously the potential role of climate in variation about the Y axis, with species in dry or cold places expected to have relatively narrow vessels for a given stem length. In other words, communities in cold, dry areas would be expected to have lower vessel diameter-stem length Y intercepts than those in warm, moist areas.

Other factors could also contribute to variation about the Y axis. About 30% have been found to be associated with vessel density, suggesting some evolutionary leeway for variation in vessel diameter and density in the context of a given stem size [49]. Some variation could be associated with leaf area supported. All else equal, plants with larger crowns would require wider vessels, so differences in crown dimensions in the context of a given stem size could explain some of this variation. Also, conduits seem to get predictably shorter stem base to tip. All else being equal, a slower pattern of acropetal shortening would be associated with longer conduits, fewer vessel termini, and lower

resistance. These species could therefore get by with narrower conduits than species with faster patterns of base-to-tip conduit shortening (drawing on 32). In this way, conduit length distributions are another factor that could systematically cause variation about the *Y* axis in the vessel diameter-stem length relationship. The relationship between Corner's rules and that between vessel diameter and stem length is also not clear. Species with low-density wood have thick terminal twigs and large leaves [89, 90]. Larger leaves mean a longer conductive path from the terminal leaf vessels to those at the petiole base. Given a constant rate of vessel widening, then larger leaves will have wider vessels at their petiole bases. This means that terminal twig vessels are likely wider in these species, assuming that all else is equal. All else is not equal, though, and species with wide leaves have stubby terminal twigs that are not as long for a given diameter as in species with small leaves. This difference in stem length-diameter allometry might "cancel out" the effect of leaf size, with the total conductive path length base-to-distal-most terminal leaf vein being ultimately similar between species of large and small leaf. So, while it is clear that vessel diameter broadly is a function of stem length and that the slope of this relationship coincides with that predicted by optimality models and therefore seems likely the result of selection favoring the maintenance of resistance constant over size increase, there is much to be understood regarding the causes of variation about the *Y* axis in this relationship.

The third issue nested within questions about growth rings is whether vessels of different size classes scale with stem length with similar scaling exponents, and this they seem to do. For example, Rosell JA and Olson ME [6] showed that the very wide vessels of lianas scale with similar exponents as the narrowest vessels. Thus, the question of broad significance is not so much ring-porous species, which represent only a very small proportion of the angiosperms and are almost all restricted to the north temperate zone [22]. Many other phenomena, such as the presence or absence of conductive imperforate tracheary elements, successive cambia, or xylem with extensive water storage capacity, cover many more species in both hemispheres than ring porosity (e.g., *Atriplex* alone), and these are major and distinctive hydraulic configurations. Ring porosity likely bulks large in studies of hydraulics because most scientists are in the north temperate zone. Instead, we suggest that the question of broadest significance remaining to be addressed is "what are the main factors causing variation about the *Y* axis in the vessel diameter-stem length relationship?"

The Rate of Within-Leaf Vessel Widening Should Vary with Height

Just as striking as the predictability of basal vessel diameter with height is that taller trees (or longer lianas) have wider terminal twig vessels (Fig. 1c). This pattern potentially involves variation with height in the vessel widening rates

within leaves. This is because terminal leaf vessel diameter, the "capillaries" in leaves, seems to be relatively invariant, i.e., all about equally and maximally narrow [86]. Assuming that they all have about the same starting diameter, then all else being equal (including leaf size), the only way to observe wider basal petiole vessel diameters, and therefore presumably terminal twig diameters, is for vessels to widen terminal vein-to-petiole base more rapidly higher and higher in a tree. Such a pattern would make adaptive sense because in this way, resistance would be lower in the leaves higher in the canopy, helping ensuring even water flow to all leaves. The predictions that leaf terminal vessel diameter should be invariant with height within and across species and that leaf vessel widening rate should be greater from the base to the top of a tree are both readily testable predictions.

Why Does Vessel Diameter Increase with Distance From the Tip Approximating a Power Law?

Vessel diameter increases with distance from the stem tip following a power law in which increase is very rapid initially and then much slower, approaching near uniformity, along the bole (Fig. 3), and this distribution presumably is of functional importance. It might be thought that vessel widening tip to base is simply the result of more and more branch vessels joining the trunk and that therefore vessels widen accordingly. However, vessels widen tip to base at a similar rate even in the unbranched trees that we have examined (not shown). This universality highlights the potential adaptive function of the power law widening rate. This rate can be thought of as dividing a tree into two partitions, one in which the vessel widening rate is nearly constant (the right part of Fig. 3) and one in which most of the widening is concentrated (left part of Fig. 3). This has the effect of concentrating most of the resistance in terminal twigs and leaves; e.g., in *Eucalyptus regnans*, up to 93% of the resistance in a tree nearly 50 m tall was found to be concentrated in the first meter of twig [50]. One tree partition can be thought of as a central superstructure made up of the trunk and branches, the more permanent parts of the tree. These have generally wide vessels that taper only gently base to tip and thus have low resistance. The other partition is made up of the terminal twigs and leaves, in which vessels taper markedly and offer high resistance. This partitioning allows a tree to adjust the resistance of terminal, disposable units in such a way as to manage water flow to the entire canopy. This management can be readily accomplished even in the face of major damage to the crown or growth in ways that significantly remodel the tree because the most disposable and readily replaced units of the tree are simply rearranged upon the efficient superstructure. In this way, it seems likely that selection should favor the concentration of most of the resistance in the most disposable parts of trees. If this is the case, then this selection pressure might be slightly

relaxed in leafless unbranched species, such as columnar cacti, which do have vessels that widen tip to base, but the exact form of this axial widening is not known.

The Significance of Variation in Within-Plant Vessel Diameter-Stem Length Scaling Exponent

We have discussed the 0.2 vessel diameter-stem length exponent as though it were invariant, but it seems likely that there is systematic variation in the exponent. It appears that as individuals reach their maximum heights, the exponent decreases. In other words, as plants reach the maximum height possible for a given site, vessels widen slightly less markedly, i.e., are relatively narrow for a given distance from the stem tip. For example, in small, actively growing maples 5 m tall, the tip-to-base widening rate was found to be >0.2 but <0.2 in a tree close to the maximum height for the study site, 0.14 at 25 m tall [87]. Similarly, in a small, vigorous ash, the pattern was >0.2 , with $D_h \propto SL^{0.3}$, and in a large *Larix decidua* close to its height limit at the site (40 m), it was <0.2 , $D_h \propto SL^{0.17}$ [2]. In a 94-m giant sequoia, several meters shorter than its neighbors, $D_h \propto SL^{0.19}$ [47]. These figures suggest that in vigorously growing plants, well below their maximum heights, the scaling exponent is often slightly >0.2 , whereas for plants at the limits of their heights, it can be <0.2 . Given the potential functional importance of this variation, understanding the causes of variation in intraindividual widening exponent seems a priority.

Does Vessel Number Increase Acropetally per Unit Leaf Area?

Some models [6, 33••] assume that vessels increase in number per unit leaf area acropetally, i.e., bifurcate or otherwise multiply in number (Table 1). If an exponent of 0.2 maintains resistance in a single conduit constant, then a fixed number of conduits could supply the same leaf area. This implies that the same number of conduits supplies the same leaf area at the tip as well as at the base of a plant. While the prediction of a fixed number of conduits per unit leaf area awaits direct testing, the observed exponent in nature of 0.2 seems to suggest that such constancy is possible.

Vessel Widening and the Safety-Efficiency Tradeoff

If it is true that basipetal vessel widening mitigates path length-induced increases in friction in such a way that resistance is maintained constant as plants grow in height, then this raises questions regarding the safety-efficiency tradeoff. The extremes in this postulated tradeoff are between vessels that are wide and conduct water rapidly but are vulnerable to embolism and narrow ones, which conduct slowly but are resistant to embolism [88]. If, however, basipetal vessel widening

is, in large part, a reflection of distance from the stem tip, with resistance remaining constant over size increases, then vessel diameter cannot be equated with flow rate independently of stem length. A small plant will have narrow conduits when small but wider conduits when large, but the flow rate per unit leaf area (“efficiency”) will remain the same.

If basipetal vessel widening does maintain resistance constant, then comparisons of efficiency between individuals need to be standardized by stem length. In Fig. 6, we show two sets of lines superimposed on the vessel diameter-stem length distribution. The black diagonal line is the best-fit regression line, and the gray diagonals are parallel to it. These parallel diagonals denote lines of equireistance. That is, moving along one of these lines, vessel diameter changes but resistance, flow rate per unit leaf area, and thus efficiency, in principle, do not. As a result, comparing segments drawn from different parts of the vessel diameter-stem length distribution corresponding to differing stem lengths will not be directly comparable. The valid comparisons to be made are along the gray verticals, which denote individuals of differing vessel diameter for a given stem length. Along these lines, path length is the same and therefore wider vessels along the entire conductive system would indeed imply greater flow rate per unit leaf area. Because wider vessels are almost certainly more vulnerable to embolism, then along these vertical axes, an efficiency-safety tradeoff should be

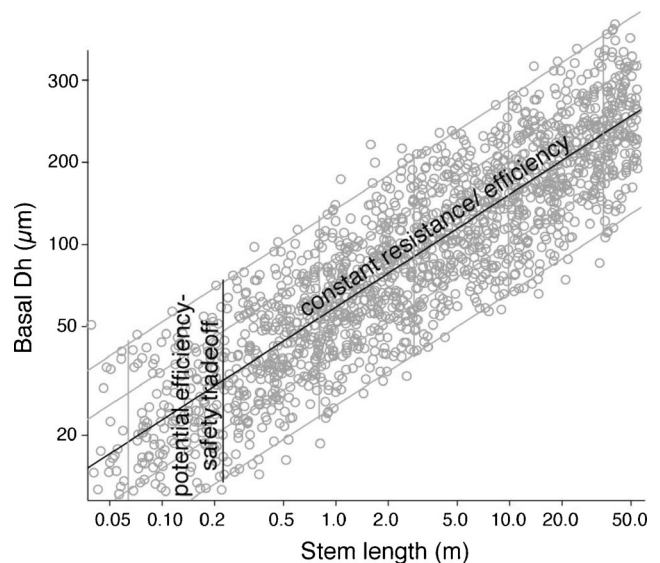


Fig. 6 Basipetal vessel widening and the safety-efficiency tradeoff, after Fig. 1. If widening does maintain resistance constant, then a vast range of vessel diameters would be associated with the same “efficiency,” understood as conductive rate per unit leaf area. The *diagonal lines* represent lines along which resistance is, in principle, equivalent; the *black line* is the best-fit regression line. Moving along one of these lines, vessel diameter changes, but resistance, flow rate per unit leaf area, and thus “efficiency,” in principle, do not. The *vertical lines*, in contrast, denote plants that have different vessel diameters for a given stem length. It seems possible that a tradeoff might emerge across individuals that differ in mean vessel diameter for the same conductive path length

detectable. In contrast, sampling widely and at random from throughout the vessel diameter-stem length distribution might not be expected to reveal a tradeoff, especially to the extent that other factors, such as pit membrane thickness, stem allometry, or even widening exponent, also vary.

This scenario remains to be tested and makes several predictions. Taller plants have predictably wider vessels, and if wider vessels are more vulnerable to embolism, then taller individuals of the same species should be more vulnerable than shorter ones. More distal parts of the same individual should be less vulnerable. This prediction seems to be confirmed in reports of cavitation preferentially affecting wider vessels in leaves [89, 90]. It predicts that an efficiency-safety tradeoff should emerge by examining samples carefully standardized by conductive path length, stem allometry, and xylem cross-sectional area. In such cross-species patterns, other factors such as pit membrane thickness and pore size seem to affect vulnerability to embolism. Factors such as leaf area, vessel density, and total vessel area should affect conductive rates. These factors are likely to vary across species, so these characteristics seem likely to explain some of the variability seen in the vessel diameter-vulnerability relationship. Given that conduit widening is most pronounced toward the stem tip (Fig. 3), then studies that focus on twigs should be most sensitive to error introduced by comparing different portions of the vessel diameter-distance from the tip curve. How to take these factors into account is still an outstanding empirical issue. However, it seems clear that not standardizing likely introduces noise that makes comparing embolism risk and other hydraulic-related traits across individuals difficult.

How to Study Adaptation: the Comparative Method, Optimality Models, and Population Biology in Plant Hydraulics

Questions such as “why do xylem conduits change their diameters predictably with plant height?” go well beyond the confines of ecology into evolutionary biology [91, 92]. Questions regarding function imply potential adaptation and as such need to be studied using the tools available for testing hypotheses regarding adaptation [93, 94]. There are three sources of data for testing adaptation hypotheses, and all three are necessary for a maximally robust test. One source consists of comparative data, which provide evidence that a given association is a general one. In the comparative method, variation is observed between species, and similar morphologies in similar selective contexts regardless of ancestral state imply convergent evolution and therefore adaptation. In the case of the vessel diameter-stem size relationship, Fig. 1 shows that given a certain stem length (the selective context) and vessel diameter (the adaptive response) can be predicted. Another source is optimality models. If selection maximizes competing performance criteria, in this case, minimizing resistance while simultaneously minimizing embolism vulnerability, then it should be possible to

predict the “least bad” combination of the competing considerations based on general biophysical principles. The finding that nature coincides with these predictions strongly supports hypotheses of adaptation. This is why the finding that broad comparative studies converge on a vessel diameter-stem length exponent of 0.2 is so significant. Finally, the third source of information is within-species studies that specifically examine the raw material of natural selection: phenotypic variation, trait heritability, and performance or fitness differences between heritable variants. This is the aspect most lacking in the study of the vessel diameter-stem length relationship. Studies of artificial selection or hormonal intervention to produce variants that differ only in their vessel diameter-stem length relation would allow testing the prediction that vessels that are “too narrow” for a given stem length should have low productivity and low fitness due to high resistance and those with vessels that are “too wide” should also have low fitness due to excessive embolism. The statement that vessel diameter scales predictably with stem size is thus just one part of series of layers of direct evidence necessary for testing hypotheses regarding the adaptive significance of variation in vessel diameter. It does not assert, as some authors have understood [95], that *all* variation in vessel diameter is explained by stem size. It instead implies that documentation of the vessel diameter-stem length relationship at a comparative scale is just one, albeit essential, source of direct evidence. As such, it only opens the door for exploration of the cause of the pattern and the contribution of other drivers in its variation.

Conclusion

Multiple sources of evidence show that mean vessel diameter should widen stem tip to base as approximately $VD \propto SL^{0.2}$ as the result of natural selection favoring the maintenance of constant hydraulic resistance as plants increase in size in ontogeny. Multiple lines of evidence—comparative studies across orders, habits, and habitats; intensive within-clade comparative work; detailed vessel widening profiles within individual trees; and hydraulic optimality models—strongly support the conclusion that conductive path length is by far the main driver of variation in mean vessel diameter. Here, we have explored a few of the multiple open questions and testable predictions highlighted by the study of vessel widening. Not only does basipetal vessel widening provide a useful methodological means of standardizing samples, but it also suggests important biological questions to address, from the effects of climate change on plant height to the action of selection on leaf characteristics. As such, vessel widening provides a useful organizing principle for understanding the evolution of plant function across the vast ranges that plants cover in size, climate, and habit and across the vast phylogenetic divergences that separate plants in their diversification across the earth.

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Compliance with Ethical Standards

Conflict of Interest Drs Rosell, Olson, and Anfodillo declare no conflicts of interest.

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