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Tip-to-base xylem conduit widening as an adaptation: causes, consequences, and empirical priorities

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Summary

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In the stems of terrestrial vascular plants studied to date, the diameter of xylem water-conducting conduits D widens predictably with distance from the stem tip L approximating $D \propto L^b$, with $b \approx 0.2$. Because conduit diameter is central for conductance, it is essential to understand the cause of this remarkably pervasive pattern. We give reason to suspect that tip-to-base conduit widening is an adaptation, favored by natural selection because widening helps minimize the increase in hydraulic resistance that would otherwise occur as an individual stem grows longer and conductive path length increases. Evidence consistent with adaptation includes optimality models that predict the 0.2 exponent. The fact that this prediction can be made with a simple model of a single capillary, omitting much biological detail, itself makes numerous important predictions, e.g. that pit resistance must scale isometrically with conduit resistance. The idea that tip-to-base conduit widening has a nonadaptive cause, with temperature, drought, or turgor limiting the conduit diameters that plants are able to produce, is less consistent with the data than an adaptive explanation. We identify empirical priorities for testing the cause of tip-to-base conduit widening and underscore the need to study plant hydraulic systems leaf to root as integrated wholes.

...as to the *Aer-Vessels*, divers questions may be asked. As how it comes to pass, that they are generally less [narrower] in the *Trunk* of the same *Plant*, than in the *Root*... Wherefore as the *Aer-Vessels* may be observed still to be dilated or widened towards the lower parts of the *Root*... So towards the upper part of the *Trunk*, to be contracted or grow smaller... the *Aer-Vessels* are somewhat, more or less, amplified in every new *Annual Ring*, or at least to a certain number of years... and so make a *Vessel* of a wider, as a more agreeable bore. Nature obtaining hereby, that the Quantity of *Aer*, shall always be answerable to the Growth of the *Plant* (Grew, 1682, pp. 130–131)

I. Introduction

Conduit diameters in the xylem of woody plants vary from < 5 to > 700 μm , and given the importance of water transport in forest productivity (Schlesinger & Jasechko, 2014; Ellison *et al.*, 2017; Šimová & Storch, 2017) it is crucial to understand the causes of this variation within individuals and across species world-wide. A key observation is that across all terrestrial vascular plants that have been studied, conduits widen predictably from the stem tip toward the stem base (Supporting Information Table S1). Within the conductive system of a single plant, the narrowest conduits are found at the terminal end of the conductive stream, in the leaves. Within the shoot–root system, mean conduit diameter is narrowest at the shoot tip (the twig tip farthest from the base; Fig. 1) (Lechthaler *et al.*, 2020). Mean conduit diameter becomes wider very quickly moving down the twig, and then the rate of conduit widening slows toward the base of the tree, continuing into the roots (Fig. 1a–c) (Lintunen & Kalliokoski, 2010; Jacobsen *et al.*, 2018; Prendin *et al.*, 2018b). As the epigraph shows, this pattern of tip-to-base increase in conduit diameter has been noticed for centuries. Despite being known for so long, tip-to-base conduit widening has yet to be recognized as one of the most widespread and functionally consequential patterns in all of plant biology, and therefore one whose causes are essential to understand. In this review, we give reason to think that this pattern is an adaptive one, a

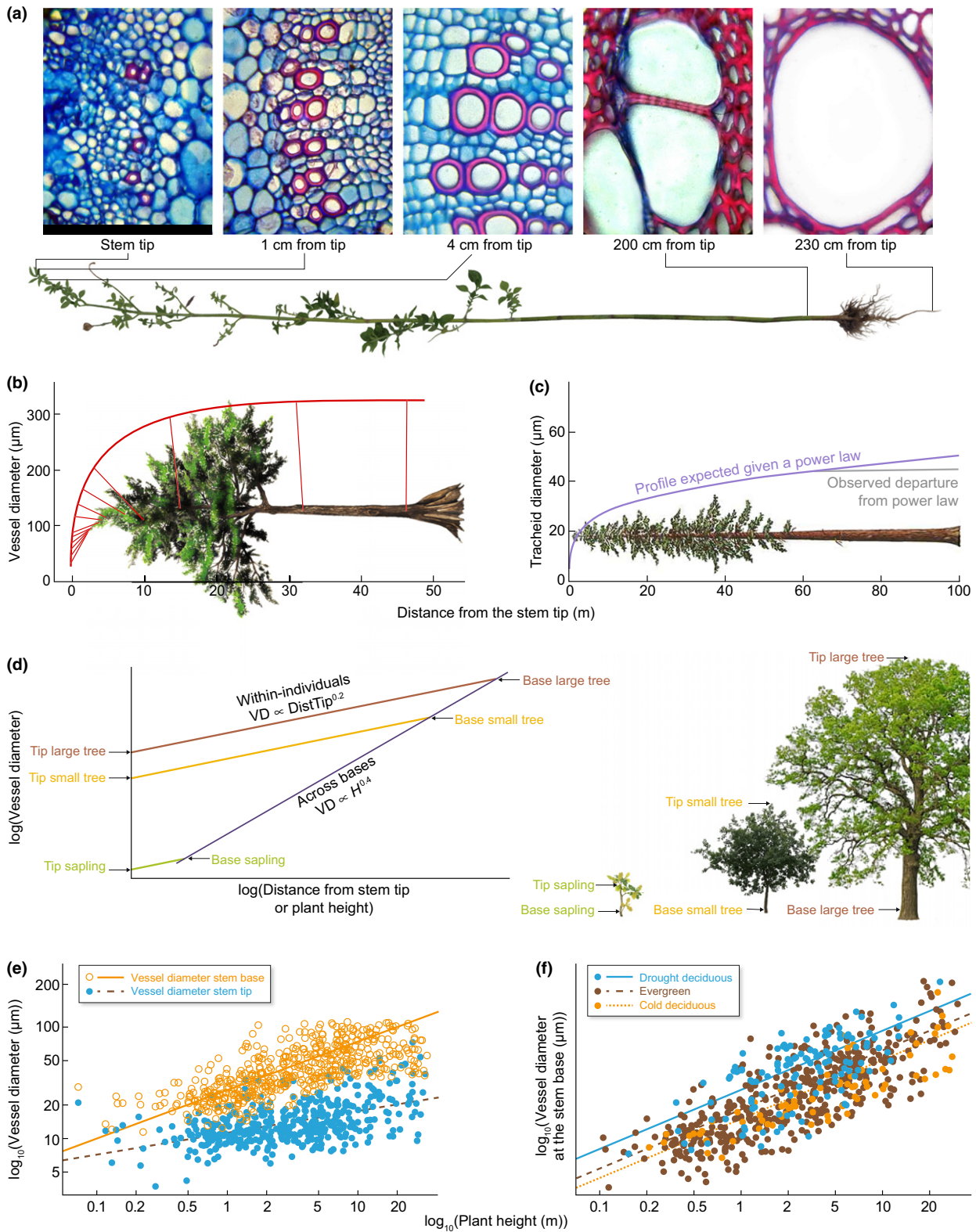
Box 1 The 'constraint–adaptation' false dichotomy

The causes of empty space about an allometric scaling line, as in Fig. 2, are often presented as a dichotomy between adaptation and the vague notion of 'constraint' (Brakefield, 2006; Olson, 2019a). With regard to the term 'constraint', we advocate avoiding it. The term has so many meanings that its use leads very easily to misunderstanding (Olson, 2012, 2019a,b). Biologists routinely discuss biophysical constraints, environmental constraints, phylogenetic constraints, developmental constraints, even selective constraints, and all have multiple definitions. Even the specific-sounding term 'hydraulic constraints' has multiple meanings (Sperry, 2000; Koch *et al.*, 2004; Petit *et al.*, 2011). The alternative is to think in terms of what is or is not developmentally possible, and the relative fitness of developmentally possible variants, reasoning that does not require using the term 'constraint', and the vagueness it inevitably introduces (Olson *et al.*, 2019; Olson, 2019c).

A complete explanation for a pattern of trait distribution in nature, such as tip-to-base conduit widening, always involves both adaptation and limits to developmental potential (Fig. 4; Olson, 2019a). All development is bound or limited in some way by factors, such as tradeoffs or enzyme kinetics, that limit the production of configurations that would otherwise be favored by selection. At the same time, among the often vast array of developmentally possible configurations, all patterns of trait distribution in nature reflect the effects of selection (Olson, 2019a). 'Empty' parts of developmental space are often the product of selection, and selection itself is the biasing of development such that low-fitness variants are rarely or never produced (Arthur, 2002; Blumberg, 2010). Fig. 4 illustrates how both limited developmental potential and selection are likely involved in tip-to-base conduit widening. Because both developmental limitations and adaptation are involved in generating any given pattern in nature, the adaptation–constraint dichotomy is a false one.

response to the hydraulic challenge imposed by increasing conductive path length as an individual stem grows longer. We discuss data that are consistent with the pattern being adaptive, and we identify crucial information still needed to test the hypothesis of its adaptiveness. We also examine, and give reasons to reject, the possibility that the pattern is

Fig. 1 Within and across-individual evidence for tip-to-base vessel widening. (a) Xylem transections showing that conduits farther from the tip are wider (*Leonotis leonurus*, Lamiaceae). The widest conduit in a given section is shown in each image. Within the stem, the vessels (stained red) are narrowest at the stem tip. Near the tip, conduits widen very quickly and within just a few centimeters are noticeably wider. They widen more slowly toward the stem base and continue widening into the roots. Bar (bottom of first micrograph), 100 μm . (b) A typical mean conduit diameter profile, from a 50 m *Ceiba pentandra*. The fitted line describing mean conduit diameter D vs distance from the stem tip L approximates a power law as $D \propto L^{0.2}$. Thin lines show the location of sampling points. (c) Especially conspicuous in larger trees, conduit widening profiles often depart from the expectations of a pure power law, being steadily narrower than expected. The cause of this departure has not been extensively explored. This example is from *Sequoia sempervirens* (Williams *et al.*, 2019). (d) Within-individual vessel widening profiles lead to predictable patterns of conduit widening with plant height across individuals. Under log transformation, power law relationships become linear. The colored lines represent tip-to-base widening profiles of the same individual as it grows taller, with the usual within-individual slope of 0.2. In vessel-bearing angiosperms, mean vessel diameter at the stem tip (the distalmost twig from the base) becomes predictably wider. This means that the Y -intercept of the within-individual tip-to-base widening profile increases as an individual grows taller. Because, within individuals, vessel diameter VD increases with distance from the stem tip DistTip as $VD \propto \text{DistTip}^{0.2}$, and because terminal twig vessel diameter VD_{tip} increases with plant height as $VD_{\text{tip}} \propto H^{0.2}$, plotting vessel diameter at the stem base against plant height H across individuals (black line) yields a slope of $VD \propto H^{0.4}$. In this way, within-individual ontogenetic patterns lead straightforwardly to across-individual patterns. (e) Illustrating across-individual relationships, mean vessel diameter at the stem base scales predictably with plant height as $VD \propto H^{0.4}$, and vessel diameter at the stem tip as $VD_{\text{tip}} \propto H^{0.2}$ across 537 species of angiosperms (Olson *et al.*, 2018b). (f) Variation about the Y -axis in the VD – H relationship across species is consistent with selection altering the relationship adaptively. For example, for the same plant height, drought deciduous species tend to have wider vessels than evergreen species. Cold-deciduous species, in turn, tend to have the narrowest vessels given the same plant height (Olson *et al.*, 2020).



nonadaptive, involving proximate, developmental conditions such as temperature, drought, and turgor limiting the possible conduit diameters ('constraint', see Box 1) that plants can

produce. We then turn to outstanding empirical priorities and methodological considerations. First, we explain what we mean by 'tip-to-base conduit widening'.

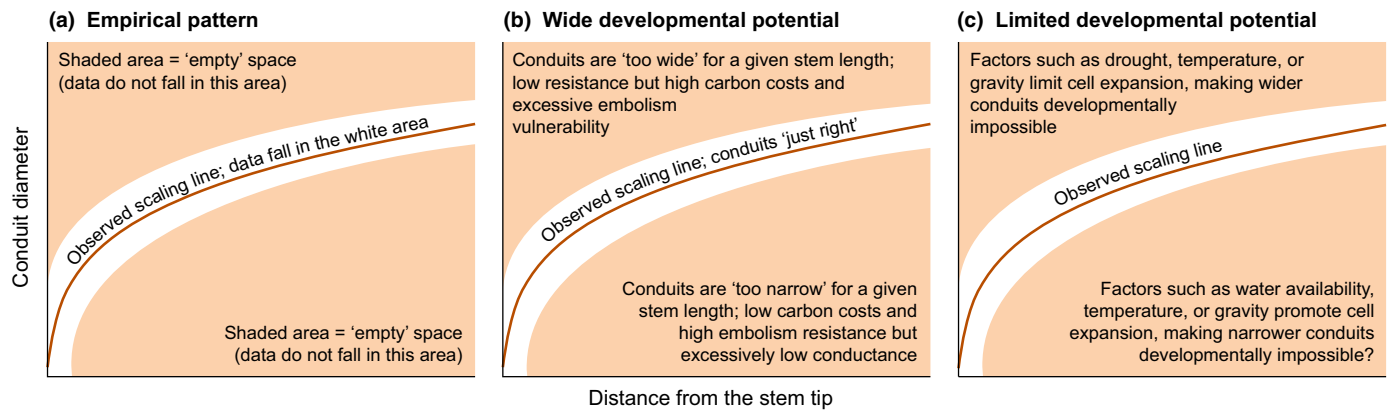


Fig. 2 Explaining tip-to-base conduit widening requires exploring developmental potential. (a) Tip-to-base conduit widening is a pervasive pattern of restricted trait distribution, with the observed data falling in a conspicuous band, and distance from the stem tip predicting mean conduit diameter at any point along the stem. Just as conspicuously, there are empty spaces above and below the scaling line. This pattern requires explanation, including what causes the empty spaces. (b) One possibility is that the spaces adjacent to the observed scaling line are readily produced developmentally but are not favored by selection because of factors such as excessive vulnerability to embolism (conduits ‘too wide’ given stem length) or excessive resistance (conduits ‘too narrow’). (c) Alternatively, one or both of the empty spaces are developmentally inaccessible; for example, factors such as gravity, hydraulic resistance, temperature, or turgor affecting cell expansion along the stem make ‘empty space’ conduit diameters developmentally impossible even though these variants would be favored by selection if they could be produced. These alternatives lead to very different explanations for tip-to-base conduit widening. Distinguishing between them requires determining whether the empty spaces are developmentally accessible or not.

II. Tip-to-base conduit widening: a pervasive pattern requiring explanation

Tip-to-base conduit widening has been recognized for centuries (Grew, 1682; Sanio, 1872; Mencuccini *et al.*, 2007; Anfodillo *et al.*, 2013; Rosell *et al.*, 2017), but detailed data have only been collected recently. The most direct data are studies of tip-to-base conduit widening from the distalmost twig to the stem base within individuals (Fig. 1a–c). Such tip-to-base widening profiles have been gathered from at least 101 species (Table S1) spanning the angiosperm phylogeny (representing 61 of the 64 or so orders) and all five gymnosperm orders, as well as ferns, clubmosses, horsetails, and spikemosses (L. Kocillari *et al.* unpublished, available from www.try-db.org as upload 388; V. Figueroa *et al.* upload 389; James *et al.*, 2003; Anfodillo *et al.*, 2006, 2012; Coomes *et al.*, 2007; Mencuccini *et al.*, 2007; Petit *et al.*, 2008, 2009, 2010, 2011, 2014; Lintunen & Kalliokoski, 2010; Bettiati *et al.*, 2012; Petit & Crivellaro, 2014; Echeverría *et al.*, 2019; Fajardo *et al.*, 2019; Williams *et al.*, 2019). This sampling spans a very wide range of plant habits from the world’s tallest trees (over 100 m tall) to desert shrubs, lianas, cacti, and arborescent monocots, as well as most of the world’s climates. Our unpublished data show that even the hydroids of the 50 cm tall moss *Dendroligotrichum dendroides* widen from tip to base. In addition to these within-individual data, evidence from 3195 angiosperm and 244 gymnosperm species shows that mean conduit diameter at the stem base scales similarly with plant height across individuals and species (V. Figueroa *et al.* unpublished, www.try-db.org upload 389; Anfodillo *et al.*, 2006; Medeiros & Pockman, 2014; Olson *et al.*, 2014, 2018b, 2020; Fajardo *et al.*, 2019; Liu *et al.*, 2019). This scaling across individuals is expected if conduits widen similarly tip-to-base within individuals (Fig. 1d). Because conduit widening is broadly similar across individuals, sampling short-to-tall individuals at comparable points on the stem (e.g. stem base and tip) will recover a predictable

pattern of conduit diameter increase with plant height even across species (Fig. 1e,f). Moreover, the well-known pattern of radial increase in conduit dimensions from pith to cambium is consistent with tip-to-base conduit widening (Malpighi, 1675; Grew, 1682; Bailey & Tupper, 1918; Olson & Rosell, 2006; Fan *et al.*, 2009; Olson *et al.*, 2014; Cabon *et al.*, 2020). Wider bases tend to have wider conduits because they usually correspond to taller stems (Anfodillo *et al.*, 2013). Conduit diameter–stem diameter data exemplifying these trends are available from at least 310 species of angiosperm (Carlquist & Grant, 2005; Olson & Rosell, 2013; Olson *et al.*, 2013). Being detected across thousands of species spanning the vascular plant phylogeny in virtually all plant habits and habitats, the pattern of tip-to-base conduit widening is pervasive. Given the dependence of conductivity on conduit diameter (Catovsky *et al.*, 2002; Scoffoni *et al.*, 2016), the pattern is unquestionably a functionally important one, but, nearly 350 yr after Grew posed the question in the epigraph, plant biologists have yet to agree on its causes. Before reviewing the evidence showing that conduit widening is almost certainly adaptive, we briefly touch on the data necessary for testing hypotheses of adaptation.

III. Testing hypotheses of adaptation: multiple layers of evidence necessary, no single experiment or datum sufficient

The hypothesis that a scaling pattern, such as tip-to-base conduit widening (Fig. 2a), is due to adaptation makes numerous predictions, all of which need to be tested for a maximally supported explanation (Olson & Arroyo-Santos, 2015). First, there must be variation in the trait of interest. This variation needs to be among individuals within the same population, because the relevant ‘competition’ involved in natural selection is within species, not between them (Olson *et al.*, 2019). This variation needs to be heritable, meaning that progeny tend to resemble their parents.

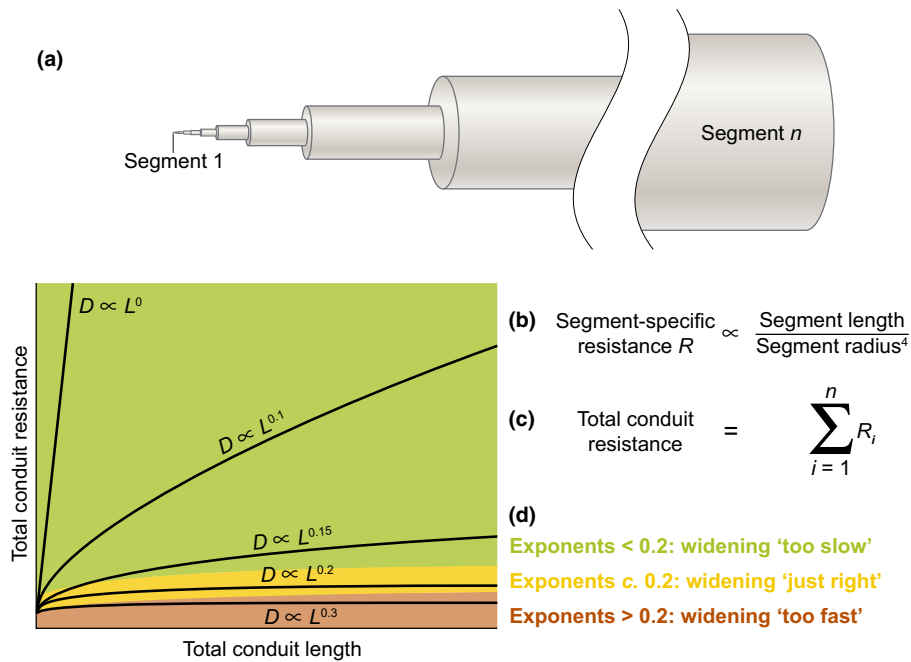


Fig. 3 Selection should favor a rate of tip-to-base conduit widening of *c.* 0.2. (a) Modeling conduit diameter *D* widening with distance from the stem tip *L* in a single conduit that is continuous from the tip to the base of a plant. The conduit is divided into cylindrical segments such that the resistance of each segment can be easily calculated. The change in diameter between segments is given by the widening exponent, varying from zero, a tube of constant diameter, to 0.3, a tube that widens quickly from tip to base. (b) Poiseuille's law gives the resistance of each segment. Resistance increases linearly with segment length and decreases with the fourth power of conduit radius. (c) The resistance of the entire conduit is the resistance of each segment summed. (d) Varying the widening exponent of the single conduit from zero to *c.* 0.3 reveals a striking pattern. Exponents of around 0.2 are associated with near-constant resistance along virtually the entire range of increase in conduit length (indicated by the curve that is level throughout most of its range). Given exponents of 0, 0.1, 0.15, 0.2 and 0.25 over a height range of 1–20 m, this simple model predicts increases in resistance of 20, 6.2, 3.6, 2.3 and 1.6 times, respectively. Scaling exponents < 0.2 are associated with conduits that are 'too narrow', with resistance increasing with conduit length. Exponents > 0.2 are also associated with near-constant resistance, but with conduits that are 'too wide'; that is, wider than necessary for achieving near-constant resistance. Being too wide means that they are potentially more vulnerable to embolism and, all else being equal, require more carbon to build. Selection should therefore favor the 'just right' 0.2 exponent. That such a simple model, of a single capillary continuous from tip to base, so closely predicts the commonly observed pattern is a remarkable observation requiring explanation.

Finally, this heritable intrapopulation variation needs to be sufficiently wide that variants with significantly different fitness can be produced (Caruso *et al.*, 2020). In the context of conduit scaling, intrapopulation variants farther above or below the commonly observed scaling line should have lower performance and fitness than conspecifics closer to the scaling line (Fig. 2b; Anfodillo *et al.*, 2016).

Data that test these predictions come from three complementary sources (Olson & Arroyo-Santos, 2015). One source is optimality models, which use basic biophysical principles to predict the compromise between two or more competing functions that maximizes some performance criterion (e.g. hydraulic conductance per carbon (C) cost). The second source is population and experimental biology, which examine variation, heritability, and fitness directly (or some performance index, such as vulnerability to embolism, that is likely to correlate with fitness). The third source is provided by the comparative method, which uses convergence, the repeated observation of similar organismal characteristics derived from differing ancestral states arising in similar selective conditions, as evidence of adaptation. All three sources of evidence are essential for testing hypotheses of adaptation, with none being more inferentially powerful than another (Olson & Arroyo-Santos, 2015).

Distinguishing between adaptive vs nonadaptive explanations for tip-to-base conduit widening is essential for understanding the evolution of plant hydraulic systems, and even in designing interventions to make plants more resistant to drought in the face of climate change. For example, if the spaces in Fig. 2 are accessible, then it indicates that it should be possible to select for differing conduit diameters for a given plant height, potentially producing more drought-resistant variants (cf. Rosner *et al.*, 2016). If these spaces are not accessible developmentally ('constraint', Box 1), then it suggests that the variants available for selection to act on are limited and that the evolutionary resilience of plants to climate change is limited to that extent. We examine, and give reasons to reject, non-adaptive interpretations. Instead, the preponderance of the evidence suggests that the best explanation for the pattern of tip-to-base conduit widening is that it is the result of adaptation, with natural selection narrowing a wider field of developmental possibilities (Figs 2–4), and we turn to this now.

IV. Evidence for adaptation: hydraulic optimality models

Some of the most compelling evidence consistent with adaptation shaping tip-to-base conduit widening comes from optimality

Box 2 Conduits widen, not taper

Tip-to-base conduit widening is often referred to as conduit 'taper', but 'widening' better describes the postulated action of natural selection shaping conduit diameter distributions. Natural selection favors very narrow conduits at the terminal end of the conductive stream. This will occur independently of tree height, leaf size, and plant habit: the narrowest conduits in the conductive system will be at the sites where water exits the xylem into the mesophyll. This vector of natural selection favoring narrow conduits at the sites of maximal diffusion out of the xylem is entirely orthogonal to that favoring conduit widening.

Following Poiseuille's law, if conduits were to remain uniform in diameter from tip to base and as a plant grows taller then resistance would increase as a linear function of conductive path length (Fig. 3). It is this increase in resistance that is buffered by conduit diameter increase. This means that conduit diameter throughout the plant body is chiefly a function of distance from the terminal end of the conductive stream (plus any furcation that might occur; McCulloh *et al.*, 2004). Selection therefore favors conduits that *widen* from a maximally and persistently narrow terminal point. The diameters at the base of a tree or at the terminal ends of the roots are simply reflections of the distance from the tip and are thus contingent on the length of the conductive path at that point. Selection does not favor a given conduit diameter at the base or in the roots independently of path length. As a result, conduits cannot be considered as narrowing or tapering from a fixed or favored basal diameter to their narrow tips. Instead, they widen from their terminal diameters as a function of path length: conduits widen, not taper.

models. Conduits are narrowest at the terminal end of the leaf xylem. Following Poiseuille's law, if these conduits were to remain narrow from their termini to the base then, as a plant grows in height and conductive path length increases, hydraulic conductance would decline as resistance increases (Vogel, 1994). Because conductance increases with conduit radius to the fourth power, small increases in conduit diameter from tip to base along the entire conductive path are, in principle, sufficient to buffer the increases in resistance caused by increasing path length, and thus minimize increases in resistance as a plant grows taller (see Box 2 on 'widening' vs 'taper'; Becker *et al.*, 2000; Mencuccini *et al.*, 2007; Rosell *et al.*, 2017).

The simplest model that makes a prediction strikingly close to the pattern of tip-to-base conduit widening observed empirically in stems and roots is of a single widened pipe stretching from the tip to the base of a plant (Fig. 3; West *et al.*, 1999; Becker *et al.*, 2000; Petit & Anfodillo, 2009; Anfodillo *et al.*, 2013; Olson *et al.*, 2018b). We turn to complexities omitted by this model later, but for now it is sufficient to note that, because resistances in series can be summed, the resistance of a single idealized tube is readily calculated as a series of cylindrical segments of different diameters (Fig. 3a–c; West *et al.*, 1999; Becker *et al.*, 2000; Anfodillo *et al.*, 2013). It is possible to express the relationship between conduit diameter D and distance from the tip along the stem of a single individual L with a power function $D \propto L^b$, where b is the tip-to-base conduit widening exponent. It describes how fast or slow the widening is from the tip to the base of a stem. When $b = 0$, the

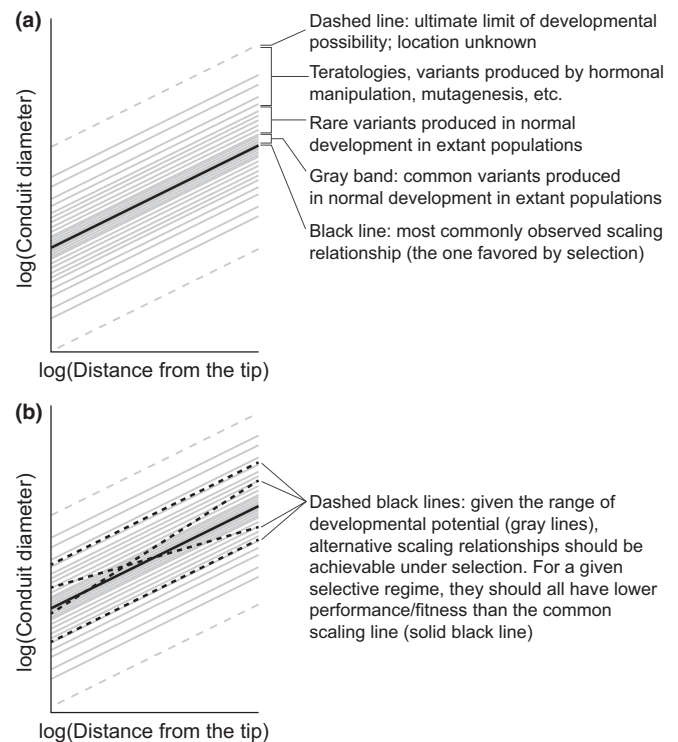


Fig. 4 Tip-to-base conduit widening, adaptation, and limits to development. (a) The notion that tip-to-base conduit widening reflects the effects of selection posits a scenario as depicted here. The figure shows one possible way that conduit diameters are bounded, both wide and narrow, for a given distance from the tip. (b) Within these bounds, it suggests that there should be sufficient developmental variation such that different slopes and intercepts can be produced. It is this range of variation that selection can act on, leading to convergence on the universal pattern of tip-to-base conduit widening observed across the vascular plants.

single tube being modeled does not widen at all, as in the pipe model (Shinozaki *et al.*, 1964a,b), and resistance increases linearly with L . When modeling conduits that widen at moderate rates (e.g. $b = 0.05$ to 0.1), substantial resistance accrues with increasing height L , but at a slower rate than in a conduit that does not widen. As b approaches 0.2 , resistances associated with increasing height become markedly reduced, and nearly constant over much of the range of height increase (Fig. 3d).

Which of these exponents should be favored by selection can be identified by appealing to the tradeoff between hydraulic conductance and vulnerability to embolism, or possibly conductance per conduit C cost. Given that values of $b < 0.2$ would result in large cumulative resistances as a plant grows taller, water delivery to the leaves, gas exchange, and photosynthesis would be similarly reduced (Catovsky *et al.*, 2002; Scoffoni *et al.*, 2016). If resistance accrued significantly with height growth, individuals that grow taller would be severely penalized. This is because individuals with markedly increasing resistance ($b < 0.2$) will experience drops in leaf-specific conductance and therefore photosynthetic productivity with height growth, and so will always be at a fitness disadvantage with respect to conspecifics in which productivity drops more slowly ($b \approx 0.2$). If conduits widen more rapidly ($b > 0.2$), the small decrease in whole-conduit resistance that this

would confer (Fig. 3d) would potentially not provide enough additional water transport and photosynthesis to offset the C required for their widening (Mencuccini *et al.*, 2007). In addition to their higher C costs, excessively wide conduits ($b > 0.2$) could also be more vulnerable to freezing and drought-induced embolism (Hargrave *et al.*, 1994; Pittermann & Sperry, 2006; Cai & Tyree, 2010; Savage & Cavender-Bares, 2013; Sevanto *et al.*, 2012; Rosner *et al.*, 2016; Jacobsen *et al.*, 2019; Liu *et al.*, 2019). Taken together, the 'just right' exponent should result in the optimization of whole-xylem resistance, vasculature construction cost, and embolism risk, and this exponent is predicted to be in the neighborhood of 0.2 (Fig. 3d).

Empirical data coincide strikingly with this prediction, with within-individual widening in the shoot-root system in all cases so far being close to 0.2 (0.1–0.3) (Anfodillo *et al.*, 2006, 2012; Coomes *et al.*, 2007; Petit *et al.*, 2008, 2009, 2011, 2014; Bettiati *et al.*, 2012; Petit & Crivellaro, 2014; Echeverría *et al.*, 2019; Fajardo *et al.*, 2019; Williams *et al.*, 2019). This result strongly suggests that natural selection has placed a premium on vascular designs with conduits that widen from tip to base in a way that minimizes the increase in hydraulic resistance that would otherwise arise as plants grow taller. Such coincidence between empirical data and optimality models is very difficult to explain without appeal to natural selection (Olson & Arroyo-Santos, 2015), strongly consistent with tip-to-base conduit widening being an adaptive pattern. Optimality models do not imply that *all* plants should follow the same pattern. Instead, if selection acts similarly in most plants, then across large samples the exponents should tend to converge on the predicted one. As we explore in the next section, variation about the predicted relationship seems likely under some situations, indeed providing key evidence in favor of an adaptive explanation for tip-to-base conduit widening.

V. Evidence for adaptation: experimental and comparative data on the range of conduit diameters that plants can produce

One way of testing the expectation that tip-to-base conduit widening is adaptive is via experiments that manipulate concentrations of auxin, which is known to be a key regulator of cell expansion, including vessels (Hacke *et al.*, 2017; Arsuffi & Braybrook, 2018). *Populus* stems treated with auxin transport inhibitors produce significantly narrower vessels (Junghans *et al.*, 2004, 2006). One experiment (Johnson *et al.*, 2018) found that blocking auxin transport changed the shape of the vessel diameter distribution and that this impacted performance, producing stems with reduced specific conductivity and potentially differing vulnerability to embolism. These results are consistent with an adaptive explanation for tip-to-base conduit widening. If conduit widening reflects limited developmental possibility (Fig. 2c) rather than adaptation, then even hormonal perturbation would be unable to alter the conduit diameter–stem length relationship. Instead of being the only configurations possible, adaptations are simply one of many possible variants, the one or ones favored by selection in a given context. So, finding that variation is developmentally possible and, moreover, that it is associated with marked

shifts in function is consistent with two of the three conditions necessary for observing selection, namely, that variation is possible and that this variation is associated with performance and likely fitness differences (Olson, 2012; Caruso *et al.*, 2020).

In addition to experiments, comparative data also provide evidence that variation in the conduit diameter–height relationship is subject to selection. If tip-to-base conduit widening is forged by selection, then alternatives to the common pattern must be developmentally possible but not favored by selection under most situations (Fig. 3). In experimental studies, researchers compare variation between control and manipulated plants. In comparative studies, the variation is observed across species (Olson & Arroyo-Santos, 2015). It is possible to use the vast differences in climate, size, life form, and other selective conditions that plants have evolved under to search for conditions that have favored variation in tip-to-base conduit widening. One example comes from a comparison between the vessel diameter–stem length relationship across 1409 samples that included 84 lianas and 340 self-supporting angiosperm species (Rosell & Olson, 2014). This study showed that lianas and self-supporting plants have similar mean vessel diameters for a given stem length. However, lianas had wider vessel diameter variances for a given stem length than self-supporting plants did. That is, for a given stem length, lianas had both significantly wider maximum vessel diameters and significantly narrower minimum vessel diameters. This pattern has been interpreted as the result of selection favoring wider maximum vessel diameter and conductively efficient vessels in these narrow-stemmed plants, as well as abundant embolism-resistant narrow ones (Carlquist, 1985a; Rosell & Olson, 2014). This observation is consistent with the space above and below the scaling line being accessible but not favored by selection in self-supporting plants (Fig. 2b). Other comparative studies have shown that, for a given height, vessel-bearing angiosperms in warmer climates have slightly wider vessels than those in cooler ones, potentially the result of selection favoring greater conductance, and thus wider vessels, for a given photosynthetic productivity, in the context of higher vapor pressure deficit (Gleason *et al.*, 2013; Olson *et al.*, 2014, 2018b; Olson, Anfodillo *et al.*, 2020; Morris *et al.*, 2018). Likewise, there is evidence that features such as leaf phenology, wood density, porosity type, and perforation plate type are associated with adaptively significant variation in conduit scaling slope and intercept (Fig. 1f; Petit *et al.*, 2016; Olson *et al.*, 2020). Together, these studies indicate that, for a given stem length, and therefore conductive path length, woody plants can produce not only narrower conduits but also wider conduits than usually observed for a given stem length. Finding that variation is possible, and, moreover, that it is functionally significant, strongly suggests that the general pattern of tip-to-base conduit widening is an adaptive one.

Data such as these, showing coincidence on the tip-to-base conduit scaling exponent predicted by a very simple optimality model (Fig. 3), as well as functionally significant variation in the conduit diameter–plant height relationship, are consistent with the hypothesis that tip-to-base conduit widening is adaptive. They suggest that variation in the scaling relationship, the first criterion for observing selection, is indeed possible (Fig. 2b). This is

suggested by experimental perturbation of development and by comparative observations suggesting that the conduit diameter–height relationship can vary under differing selective conditions. Coincidence on the exponent predicted by optimality models is consistent with the observed scaling pattern being the one favored by selection. These observations are consistent with the second and third conditions necessary for observing selection; namely, that developmentally possible variation is also heritable and that it is associated with performance and fitness differences. Numerous crucial points, however, remain to be tested. One of these is to consider the possibility that the tip-to-base scaling pattern is not an adaptive one (Fig. 2c).

VI. Conduit widening is unlikely to be nonadaptive

Conduit diameter varies conspicuously with factors such as temperature and water availability, often throughout the growing season (Cook & Kairiukstis, 2013), so it is necessary to examine the possibility that the slope and intercept of tip-to-base changes in diameter might be a consequence of these external factors, rather than an adaptation. Wood anatomists frequently document features ranging from abnormal conduit diameters to the production of resin canals, parenchyma bands, or suberized cells in response to traumas such as sudden drought, flash freezes during the growing season, and wounding (Wilkes, 1986; Carlquist, 1988, 1989, 2001; Taylor & Ryberg, 2007). Others suggest that accumulating hydraulic resistance and gravity with height could lower turgor below that necessary for cell expansion and lead to reduction of cell dimensions at the tops of tall trees (Ryan & Yoder, 1997; Koch *et al.*, 2004). All of these potentially offer candidates for nonadaptive causes of tip-to-base conduit widening.

The key diagnostic for distinguishing adaptive vs nonadaptive causes in the sense we invoke here (Fig. 4) is whether or not plants can produce alternative scaling relationships, and whether or not the alternatives have (or would have if they could be produced) higher fitness than the commonly observed relationship. In the case of adaptation, alternatives to the commonly observed relationship should be producible, but not commonly observed in natural populations because they have low fitness (Fig. 2b; Olson, 2012; Olson & Arroyo-Santos, 2015; Anfodillo *et al.*, 2016; Rosell *et al.*, 2017). If conduit diameters are limited nonadaptively by gravity, drought, cold, or hydraulic resistance, then this implies that, given the conditions under which conduits are expanding, production of wider conduits is impossible, even though these would be favored by selection (Fig. 2c). For example, Cabon *et al.* (2020) modeled tracheid expansion based on water potential. They found that ‘tracheid enlargement and final dimensions can be modeled based on the direct effect of water potential on turgor-driven cell expansion’ (p. 209) and hypothesized that ‘the gradual pressure drop along the hydraulic path (Woodruff *et al.*, 2004; Meinzer *et al.*, 2008) [the cited authors attribute the drop to gravity and hydraulic resistance] appears to be an adequate candidate to explain the universal tree base-to-top tapering of xylem conduits (Anfodillo *et al.*, 2006, 2012; Olson *et al.*, 2014), as well as limitations to tree height (Koch *et al.*, 2004)’ (p. 218).

That Cabon *et al.* (2020) invoke only developmental conditions and causes, and not the fitness impacts of heritable intrapopulational variation, suggests the possibility that factors such as water availability, gravity, and hydraulic resistance could cause tip-to-base conduit widening in ways that are nonadaptive. The scenario of Cabon *et al.* (2020) implies that water potential limits the possible range of tracheid diameters that can be produced and that alternative conduit diameters are developmentally impossible. Similarly, studies that suggest that conduit diameters are limited by gravity and hydraulic resistance at the tips of tall trees (Ryan & Yoder, 1997; Koch *et al.*, 2004; Woodruff *et al.*, 2004; Woodruff & Meinzer, 2011) postulate situations in which conduit diameters are limited nonadaptively. If this were true, it would imply that tall trees *cannot* produce wider conduits even though these would result in further height growth, greater leaf-specific conductivity, and higher fitness. In contrast to this perspective, if the conduit diameters observed in these studies are adaptive, this would suggest that plants *can* produce wider or narrower conduits in a given situation, but that under the same selective conditions these variants would have lower fitness than the observed ones (Fig. 2b).

Available data suggest that under normal conditions, and especially with regard to tip-to-base conduit widening, conduit diameter is finely tuned by adaptation. This means that plants are, under almost all conditions, producing the conduit diameters favored by selection out of a much wider array of possible diameters (as in Fig. 2b), rather than being limited nonadaptively by the conditions they find themselves developing in (as in Fig. 2c). Even under the extreme conditions of maximal plant height, there is little evidence to suggest that path length and gravity reduce conduit dimensions. If this were the case, then taller trees, especially ones close to their height limits, should have increasingly narrow conduits at the tips of topmost twigs than shorter individuals do, but data do not bear out this prediction. In a study in *Sequoia* and *Sequoiadendron*, Williams *et al.* (2019) found that terminal twig tracheid diameter showed no decline within individuals well below maximum height to individuals over 100 m tall. Similarly, across species, mean tracheid diameter in the terminal twigs of gymnosperms either increases or shows no tendency to decrease with height (Prendin *et al.*, 2018a), and across angiosperms, terminal twig vessel diameter actually increases with plant height (Fig. 1d,e; Zach *et al.*, 2010; Olson *et al.*, 2014, 2018b, 2020). These patterns are all consistent with plants producing the adaptively favored conduit diameter along the entire conductive path, rather than gravity and path length imposing nonadaptive limits to conduit diameter.

Similarly, temperature and water availability do not appear to modify the conduit diameter–plant height relationship in ways consistent with nonadaptive limitation of development. If water availability limited the ranges of conduit diameters that can be produced, then plants in drier sites would have narrower conduits for a given plant height than those in moist ones, but this is not the case. In a study of tip-to-base vessel widening of two angiosperms across a very marked mean annual precipitation gradient (500–2300 mm), Fajardo *et al.* (2019) found that both the slope and intercept of tip-to-base widening profiles was unchanged. Lechthaler *et al.* (2018) found similar results across seven species

of *Acacia* across a different precipitation gradient (330–1110 mm). One study reported marginal differences in intercept ($P = 0.02$) between *Fraxinus* trees growing in soils with high vs low moisture retention (Kiorapostolou & Petit, 2019). In temperate conifers, various researchers have found constant tip-to-base conduit widening across gradients of nutrient availability and temperature (Coomes *et al.*, 2007; Piermattei *et al.*, 2020), and even across trees subject to experimental manipulation of CO₂ concentration and soil temperature (Prendin *et al.*, 2018b). Similarly, water availability did not affect the slope or the intercept of the relationship between mean vessel diameter per species and stem length across hundreds of angiosperm species spanning most of the world's climates (Olson *et al.*, 2014, 2018b; Morris *et al.*, 2018). This constancy of scaling would be impossible if water availability nonadaptively limited the range of vessel diameters that can be produced. With regard to the role of temperature in limiting the developmental range of conduit diameters, Petit *et al.* (2011) heated growing tips in wild spruce trees growing at their upper elevation limit for 2 yr. They found that heated and unheated plants produced the same total range of tracheid diameters. Similar total ranges would only be possible if the temperatures normally encountered by these trees did not limit the range of tracheid diameters that the trees could produce in development.

Together, these studies indicate that tip-to-base conduit widening is most likely adaptive. The consistency with which similar conduit diameter–plant height scaling relationships are observed across very large environmental gradients (Coomes *et al.*, 2007; Lechthaler *et al.*, 2018; Olson *et al.*, 2018b; Fajardo *et al.*, 2019) gives no reason to suspect that tip-to-base conduit widening is a nonadaptive result of limiting developmental conditions (Fig. 2c; the dashed lines in Fig. 4). Rather than being the inevitable result of environmental conditions, the production of narrow conduits during dry or cold conditions is consistent with the possibility that narrower conduits are more resistant to both freezing (Pittermann & Sperry, 2006; Savage & Cavender-Bares, 2013; Sevanto *et al.*, 2012) and drought-induced embolism (Hargrave *et al.*, 1994; Cai & Tyree, 2010; Liu *et al.*, 2019) and therefore favored by selection. Even given this evidence, numerous questions remain to be addressed.

VII. Key empirical priorities

Observations such as convergence on the predicted $D \propto L^{0.2}$ exponent are only plausibly explained by appeal to selection narrowing a wide field of developmental possibility (Figs 2b, 3). However, despite convincing evidence that conduit widening is adaptive, crucial data remain to be collected, and we highlight important priorities here.

1. Are the empty spaces developmentally accessible or not? Variation in intercept

By far the most important outstanding empirical priority in probing the adaptive origin of tip-to-base conduit widening is to test the developmental accessibility of the empty spaces around the empirical allometric scaling pattern. If selection is responsible for

tip-to-base conduit widening, it means that there is (or at least once was) sufficient variation in developmental potential across the individuals of a species such that alternative log–log tip-to-base conduit widening patterns are possible (Fig. 4). The auxin inhibitor experiment of Johnson *et al.* (2018) is informative because it shows that the ‘conduits too narrow’ portion of Fig. 2b is eminently reachable. The ‘too wide’ area (above the curve) remains to be explored in detail. One approach to test the accessibility of this region is artificial selection. Vascular plants of appropriately short generation times could be bred such that those with relatively wide and relatively narrow conduits for a given stem length could be produced (cf. Rosner *et al.*, 2016). This would demonstrate the crucial presence not only of developmentally possible variation within populations but also that this variation is heritable. Hormonal and genetic manipulation in the spirit of Johnson *et al.* (2018) and Scarpella (2017) would allow mapping of a likely even wider space of developmental possibilities than artificial selection.

2. Are the empty spaces developmentally accessible or not? Variation in scaling exponent

In addition to the intercept, it also remains to be determined directly whether selection can alter the tip-to-base widening exponent (Stillwell *et al.*, 2016). There is some evidence that, within a species, taller individuals have slightly lower tip-to-base scaling exponents (Mencuccini *et al.*, 2007; Petit *et al.*, 2008). It could be that increases in leaf size from small to large plants lead to longer conductive path lengths in the leaves. This would lead to wider conduits at the petiole base in leaves, and thus wider terminal twig conduit diameters. A lower scaling exponent would then result in the favored conduit diameters at the stem base. Congruent with this expectation, in palms, most conduit widening occurs in their very large leaves, with widening in the stem being very slight (Petit *et al.*, 2014). These examples suggest that the conduit widening rate in the stem can vary in ways that are adaptive, but the pervasiveness and cause of these patterns have not been explored. The across-species vessel diameter–stem length scaling slope does appear to vary across some selective contexts; for example, with the earlywood vessels of ring porous species scaling with a steeper exponent than the latewood vessels (Olson *et al.*, 2020). Another way that the widening exponent could vary adaptively is suggested by models that indicate the tip-to-base widening exponent can vary if conduit number varies across stem segments (McCulloh *et al.*, 2003, 2004; Savage *et al.*, 2010; Rosell *et al.*, 2017). Whether variation in the scaling exponent (*c.* 0.1–0.3) is systematically related to variation in conduit number remains to be explored. All of these data suggest that slope can vary under selection, but further testing, as with artificial selection experiments, would be ideal. In addition, all published data so far regarding tip-to-base conduit widening have examined terrestrial plants, in which water must be brought to the leaves all the way from the roots. However, it seems possible that, in submerged aquatic plants, selection favoring the minimization of resistance along the entire path length might be relaxed and different exponents might be observed (Drobnitch *et al.*, 2015), a result that would be strongly consistent with the notion that the

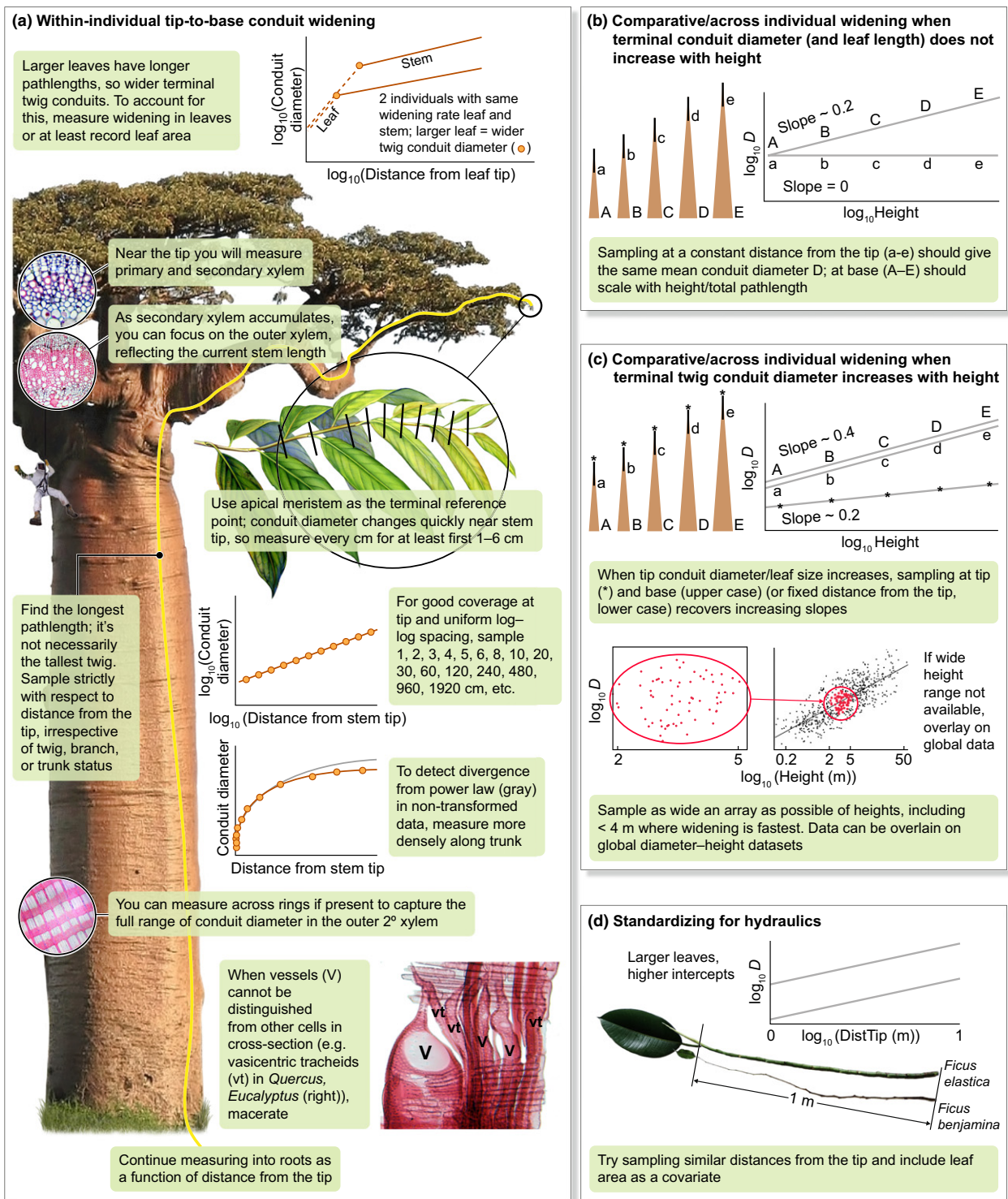


Fig. 5 Considerations for sampling. Many details remain to be worked out regarding optimal sampling, and we provide some working considerations here. (a) Within-individual tip-to-base profiles. Ideally, sample quite densely at the stem tip because conduit diameter changes very rapidly there. To identify true conduit diameter distributions, expert anatomical work is needed, and image analysis software will be unreliable for measuring all but the simplest anatomies. (b, c) Sampling across individuals (e.g. stem tip and base samples vs plant height). (b) When terminal twig conduit diameter D_{tip} does not increase with plant height L (e.g. when leaf size does not increase with height), then conduit diameter at the base scales with height as about $D_{\text{base}} \propto L^{0.2}$. Sampling a fixed distance from the tip should be comparable across individuals. (c) However, when D_{tip} does increase with plant height, the increase in 'starting diameter' (i.e. conduit diameter–plant height Y -intercept) needs to be taken into account (see Box 3). Because there is wide variation about the Y -axis (Fig. 1e,f), it is essential to measure as wide a height range as possible; if a wide range is not available and no relationship is apparent, data can be overlain on available global data (e.g. Olson *et al.*, 2020). (d) Much remains to be established regarding best practices for standardizing twig samples, as for measurements of vulnerability to embolism. Collecting samples at a constant distance from the twig tip, and including leaf size as a covariate in analyses (see Box 3), would be an important step toward more comparable sampling. Round insets in (a) top to bottom: *Vahlia capensis*, *Fraxinus uhdei*, *Trochodendron aralioides*.

commonly observed tip-to-base scaling exponent across terrestrial plants is one favored by selection.

3. Do empty space variants have lower fitness than the commonly observed ones?

Whether achieved by natural or artificial selection or by perturbation of development, creating 'empty space' variants would allow testing directly the prediction that variants in the 'too wide' and 'too narrow' spaces should have lower performance and fitness with respect to conspecifics along the usual scaling line (Fig. 2b; Anfodillo *et al.*, 2016). Selective factors leading to 'empty space' potentially include increased vulnerability to embolism in the 'too wide' zone and reduced stomatal conductance in the 'too narrow' zone. Finding that variants in the 'too wide' and 'too narrow' zones can be produced developmentally, that they are heritable, and that they are associated with lower performance or fitness than those along the normal scaling line would provide the outstanding layers of evidence necessary to clinch the adaptive interpretation of tip-to-base conduit widening.

4. What is selection acting on in favoring tip-to-base conduit scaling?

In most questions of adaptation, determining why certain variants are associated with greater or lesser fitness is a perennial challenge (MacColl, 2011), and tip-to-base conduit widening is no exception. The scenario we sketched herein, with selection minimizing the increase in hydraulic resistance with height growth, is a very general one and invokes numerous points that remain to be tested in detail. Gravity and its contribution to resistance, for example, does not appear to be the main driver favoring conduit widening. If gravity were the main selective agent, then prostrate, climbing, and other nonvertical habits would have differing conduit widening patterns, but they are apparently identical to erect self-supporting plants (Rosell & Olson, 2014; see also Domec *et al.*, 2019). However, the relative influences of gravity and pathlength on conduit widening remain to be disentangled in detail.

Given the strong relationship between hydraulic conductance and photosynthesis (Catovsky *et al.*, 2002; Scoffoni *et al.*, 2016), and photosynthesis and C gain (Kikuzawa & Lechowicz, 2006; Selaya & Anten, 2010; Stephenson *et al.*, 2014), it seems likely that tip-to-base conduit widening, such that hydraulic conductance remains constant per unit leaf area with height growth, is a result of selection favoring the maintenance of whole-plant productivity. Within a species, individuals whose leaf-specific photosynthetic productivity declines with stem length increase would experience a continual decline in surplus C directed to growth and reproduction. Individuals with the lowest decline in photosynthetic productivity per unit leaf area with height growth would maintain the largest C surpluses as they grow taller. These individuals would, as a result, have higher growth rates and produce more propagules, meaning that in any given population, selection should always be expected to favor individuals with the lowest decline possible in leaf-specific photosynthetic productivity with height growth. This notion remains to be tested in detail, though some data are

consistent with it. One observation is that tree crowns fix a relatively similar amount of C across species over a growing season (Poorter *et al.*, 1990; Selaya & Anten, 2010; Michaletz *et al.*, 2014; Stephenson *et al.*, 2014). Others document wood production that is apparently constant per unit leaf area as trees grow in height (Sillett *et al.*, 2010). Such constancies would be impossible if the whole-plant net CO₂ assimilation rate dropped appreciably per unit leaf area with height growth. Congruent with this idea, in an experiment in the tropical tree *Moringa oleifera*, Echeverría *et al.* (2019) found that vessel diameter and number change with height growth in a way that maintained hydraulic conductance constant with leaf area. Some researchers, however, have documented drops in photosynthetic productivity and stomatal conductance with height growth (Koch *et al.*, 2004; Ambrose *et al.*, 2016). Maintaining constant (or increasing) conductance with height growth is likely especially important for forest tree species, which grow up through a dark and humid understory into much higher radiation environments with higher evaporative demand (Gleason *et al.*, 2018b).

In the same way, selection plausibly favors conduits that widen enough but not excessively via a tradeoff between conductance and C cost. Given conduits of identical length, a conduit that widens 'too quickly' (e.g. $b > 0.2$) would achieve very nearly the same whole-path conductance as a conduit that widens at the optimal rate ($b \approx 0.2$), but would require more cell wall and therefore more C to construct. Any C invested beyond that necessary for a given conductance cannot be invested in further growth and reproduction. As a result, selection plausibly minimizes C cost for a given conductance (Mencuccini *et al.*, 2007).

5. Why does a simple widened pipe model predict the tip-to-base exponent so well?

The prediction of a tip-to-base widening rate of $D \propto L^{0.2}$ (Fig. 3) excludes much biological detail but nevertheless coincides strikingly with empirical observations, and how this happens remains an important research question. Real conduits are finite in length, have irregular internal sculpturing and constrictions that increase resistance, and water must pass through interconduit pit membranes (Comstock & Sperry, 2000; Carlquist, 2001; Becker *et al.*, 2003; Pittermann *et al.*, 2010; Brodersen *et al.*, 2014; Schulte *et al.*, 2015; Li *et al.*, 2016; Medeiros *et al.*, 2019); and, as explained in the following subsection, there are reasons to expect that selection can act on the relationship between conduit diameter and number (McCulloh *et al.*, 2003, 2004, 2009; Mencuccini *et al.*, 2007; Gleason *et al.*, 2018a). However, even though the $D \propto L^{0.2}$ model does not include these variables (Fig. 3), empirical observations converge remarkably on the predicted exponent. This suggests that the resistance imposed by vessel length variation, internal sculpture, and pits must scale isometrically with resistance, and thus conduit diameter, along conduits, and there is some evidence consistent with this expectation (Sperry *et al.*, 2005). In a recent study along the length of a large giant sequoia, Lazzarin *et al.* (2016) found that tracheid diameter scaled with the expected $D \propto L^{0.2}$ (see also Becker *et al.*, 2003). Remarkably, the areas of the pit apertures, the torus, and margo also scaled with distance from the tip with a 0.2

exponent, with the sum per tracheid of the open area of the margo scaling isometrically with tracheid lumen area. Though much remains to be explored, the results of Lazzarin *et al.* (2016) suggest that selection favors conductive systems in which features vary tip to base in such a way that increase in resistance is minimized with height growth, bearing out the predictions implied by the simple widened pipe model (Fig. 3).

6. What is the role of 'furcation'? Achieving conductance via conduit diameter vs conduit number

Murray's law shows that conductive systems in which conduits coalesce tip to base, as from capillaries to blood vessels to arteries to the aorta in mammals, have much lower construction costs per network conductance than those divided into parallel conduits (Murray, 1926). This coalescence ('furcation') is conspicuous in leaves, with fine terminal conduits quickly coalescing into fewer and fewer conduits per unit leaf area (McCulloh *et al.*, 2003, 2009; Gleason *et al.*, 2018a; Lechthaler *et al.*, 2019). Some studies have found that there is no coalescence in stems (Bettiati *et al.*, 2012), and even in species that do exhibit coalescence (McCulloh *et al.*, 2004) it is much less marked than in leaves. However, given that the rate of coalescence is needed to predict the optimum rate of conduit widening, and that the rate of coalescence is largely unknown across species, this remains an important research priority.

7. What is the role of variation in leaf size?

The influence of leaf length on tip-to-base conduit widening remains to be explored in detail, but studies so far suggest that leaf size is a major factor in causing variation in terminal twig conduit diameter (Lechthaler *et al.*, 2020). Longer leaves have longer path lengths, and thus wider conduits at the leaf base (Fig. 5a,d). Conduits in leaves typically widen faster than in the stem, often about twice as fast, so small differences in leaf size will lead to large differences in petiole base conduit diameter and likely terminal twig conduit diameter (Sack *et al.*, 2012; Gleason *et al.*, 2018a; Lechthaler *et al.*, 2020). Even given the same tip-to-base conduit widening exponent in the stem, individuals in which terminal twig conduit diameter is wider will have wider conduits throughout (Fig. 5a,d). Congruent with this expectation is the finding that across species, lower wood density is associated with wider vessels given plant height (Olson *et al.*, 2018b). Lower wood density is associated with longer leaves (Olson *et al.*, 2018a), and if longer leaves are associated with longer pathlengths, wider petiole base conduit diameters, and therefore wider terminal twig conduit diameters, then the leaf size-twig size spectrum (Westoby & Wright, 2003) could be related to variation about the Y-axis in tip-to-base conduit widening profiles (Fig. 5a,d), another expectation remaining to be explored.

8. How do conduit widening and plant height interact with adaptation to climate and climate change?

If taller plants have predictably wider conduits and if wider conduits are more vulnerable to embolism, then height should be a crucial variable involved in adaptation to climate, plastic

acclimation to microsite conditions, and plant responses to climate change (Coomes *et al.*, 2007; Pittermann *et al.*, 2014; Olson *et al.*, 2018b). Assuming that wider conduits are more vulnerable to drought-induced embolism – and there is evidence consistent with and equivocal with respect to this possibility (Hargrave *et al.*, 1994; Cai & Tyree, 2010; Jacobsen *et al.*, 2019; Liu *et al.*, 2019) – this suggests that individual plants will plastically grow to the height corresponding to the conduit diameter permitted by microsite conditions and remain at that height unless conditions change. This would also suggest that, at the same site and within a given species, individuals with the widest conduits for their height should also be more vulnerable to embolism. Consistent with this notion a survey of *Pinus sylvestris* showed that individuals that were in declining health at the same site had wider conduits (Kiorapostolou *et al.*, 2020). Conversely, selecting individuals of a species with relatively narrow conduits for a given height (incurring into the lower shaded space in Fig. 2) should result in more drought-resistant variants (cf. Rosner *et al.*, 2016). Variation in height-specific conduit diameter might also explain the shedding of terminal branches commonly observed during episodes of forest dieback (McDowell *et al.*, 2008). Trees that shed their terminal branches (Rood *et al.*, 2000) would not only reduce transpirational demand on the conduit network, but the remaining branches would also have shorter path lengths and therefore also narrower and more drought-resistant conduits.

9. How does selection favoring tip-to-base conduit widening interact with storage and support functions of the xylem?

Further aspects not included the single capillary model (Fig. 3) are the mechanical and storage roles of secondary xylem, but it is clear that the conduction-storage-support tradeoff is key to understanding xylem evolution (Montes-Cartas *et al.*, 2017; Pratt & Jacobsen, 2017). That vessels scale similarly across self- and nonself-supporting plants suggests that mechanics has no influence on the rate of tip-to-base conduit widening (Rosell & Olson, 2014; see also Domec *et al.*, 2019). Recent studies in angiosperms (Olson *et al.*, 2014, 2020) indicate that vessels become slightly more abundant per square millimeter at the base with increase in tree height than would be expected given the simple geometric tradeoff in which vessel density should scale linearly with the square of vessel diameter (Ewers *et al.*, 2007; Zanne *et al.*, 2010). This suggests the possibility that trees, as they get taller and have a greater xylem superstructure providing support, divert some C from support cells to vessels (Olson *et al.*, 2014). So, though there is some indication that selection acting on mechanical support is involved in C allocation patterns that affect tip-to-base conduit widening, the relationship between such scaling and mechanical support, as well as the storage role of xylem, has only begun to be explored.

10. Does plant size or cambial age determine conduit diameter?

Although there are compelling reasons to think that plant size, via conductive path length, is a central factor affecting conduit

diameter, cambial age is often regarded as affecting diameter (Bailey & Tupper, 1918; Lenz *et al.*, 2010; Li *et al.*, 2019; Rodriguez-Zaccaro *et al.*, 2019), though there is, as far as we are aware, no reason to expect age *per se* to predict conduit diameter beyond its correlation with plant size (Carrer *et al.*, 2015). Poiseuille's law provides solid theory for expecting that increasing path length should lead to increased resistance with height growth and that tip-to-base conduit widening can buffer this increase in resistance. Identifying whether size or age is the main predictor of conduit diameter could be readily tested by examining individuals of the same species that are of similar size but different age, and similar ages but different sizes, as in Rosell & Olson (2007), who used such an approach to show that stem biomechanics in a species of small tree is predicted only by stem size, not age. Likewise, Cary *et al.* (2020) provide an example of an ideal natural experiment in which to test the importance of size vs age on conduit diameter. If cambial age *per se* can in fact affect conduit diameter, then the development of solid theory outlining the age–diameter causal mechanism would be an important priority.

VIII. A change in the plant hydraulics paradigm: from cross-sections to entire path lengths

That the pervasive pattern of tip-to-base conduit widening is likely adaptive underscores that natural selection acts not on what is seen in a single stem cross-section or stem segment, which are the usual subjects of plant hydraulic studies, but instead acts on the characteristics of the entire conductive system, from roots to leaves, as an integrated functional unit (Prendin *et al.*, 2018b; Bouda *et al.*, 2019; Brodersen *et al.*, 2019; McCulloh *et al.*, 2019; Roddy *et al.*, 2019). This possibility requires fundamentally rethinking the way that plant hydraulic traits are studied (McCulloh *et al.*, 2019; Soriano *et al.*, 2020).

1. Methodological implications

That conduits scale tip to base broadly similarly across species provides a means of increasing comparability of measurements across individuals. Within-individual tip-to-base conduit widening profiles can be collected following the longest path length in an individual (Fig. 5a). Because conduit diameter changes quickly near the stem tip, it is important to sample frequently in this region to detect these changes. Across individuals or species, anatomists traditionally compare conduit diameters without taking plant height into account. This means that finding that one species has wider conduits than another could simply reflect that one species is typically taller than another. Anatomical and hydraulic measurements can thus standardize for tip-to-base conduit widening, so that it can be stated that, *for a given height*, species A has wider conduits than species B (Fig. 5b). Comparisons based on similar distances from the tip, taking leaf size increases into account, promise maximally comparable measurements (Fig. 5; Box 3; Soriano *et al.*, 2020). Soriano *et al.* (2020) provide an example in which on comparing the vulnerability to embolism of basal segments from tall individuals of *Casimiroa* (Rutaceae) with short individuals of *Moringa* (Moringaceae) it appeared that *Casimiroa*

Box 3 Statistical resources for studying tip-to-base conduit widening

- (1) D , conduit diameter
- (2) DistTip, distance from the stem tip
- (3) L , total plant height, stem length, or conductive path length

Within-individual tip-to-base widening profiles

For one individual, the relationship is often reflected well by:

$$\log_{10}D \approx \log_{10}(\text{DistTip})$$

For profiles from multiple individuals, including height can help take into account any tendency for Y -intercept to increase with height; for example, if leaf length increases with height:

$$\log_{10}D \approx \log_{10}(\text{DistTip}) + \log_{10}L$$

Slopes may lower with height, so it is likely necessary to nest data within individuals.

Comparative/across-individual sampling

This strategy samples similar points across individuals; for example, at the stem tip D_{tip} and at the base D_{base} . How both scale with L (as in Fig. 1d–f) can be studied with:

$$\log_{10}D_{\text{base}} \approx \log_{10}L \text{ (model 1)}$$

$$\log_{10}D_{\text{tip}} \approx \log_{10}L \text{ (model 2)}$$

If D_{tip} increases with height, then the $\log_{10}D_{\text{base}} \approx \log_{10}L$ slope will increase more steeply than the within-individual tip-to-base widening rate (Fig. 1d). Here are two strategies for inferring the within-individual tip-to-base widening rate (Anfodillo *et al.*, 2006):

- a Fit models 1 and 2; subtract slope of model 2 from model 1.
- b Calculate W (for 'widening') by dividing mean $D_{\text{base}}/D_{\text{tip}}$ for each sample; fit $\log_{10}W \approx \log_{10}L$.

If leaf length varies across individuals, terminal twig conduit diameter will vary, leading to differences in slope between within-individual and across-individual sampling (Fig. 1d). This effect can be tested for with:

$$\log_{10}D \approx \log_{10}L + \log_{10}(\text{Leaf length})$$

Such an approach can be used for testing for the effects of other continuous variables, such as wood density (Olson *et al.*, 2018b, 2020), or categorical variables, such as perforation plate type or vesturing (Medeiros *et al.*, 2019):

$$\log_{10}D \approx \log_{10}L + \text{categorical|continuous variable}$$

For hydraulic measurements

Sampling a constant distance from the stem tip (e.g. 50 cm) and including leaf size as a covariate should produce informatively comparable results; for example, for P_{50} , the pressure at which 50% conductivity is lost:

$$\log_{10}(P_{50} \text{ at } 50 \text{ cm from tip}) \approx \log_{10}(\text{Leaf size})$$

was more vulnerable than *Moringa*. However, when individuals of *equal height* were compared, it was clear that *Moringa* was markedly more vulnerable than *Casimiroa*. It therefore seems likely that standardizing for tip-to-base conduit widening and plant height could reduce at least some of the notorious noise in vulnerability curves (Fig. 5; Box 3; Olson *et al.*, 2018b; Soriano *et al.*, 2020). Along these lines, it is a common practice in studies of plant hydraulics to standardize twig samples by diameter. Because species commonly differ in branch length–diameter allometry – with

species with lower wood density having thicker branches (Rosell *et al.*, 2012; Olson *et al.*, 2018a) – standardizing by twig diameter necessarily introduces a great deal of variation in conductive path length, and therefore in conduit diameter. Careful standardization of twig samples is particularly important because conduit diameter changes rapidly over such short distances near the stem tip (Figs 1,5), and so even small variation in the distance from the tip in twig samples is associated with large differences in conduit diameter. Sampling with respect to distance from the ground (Li *et al.*, 2019) will not standardize measurements because widening begins at the stem tip and proceeds through the base into the roots, making distance from the base an arbitrary reference point (Box 2; Prendin *et al.*, 2018b). Even what index of conduit diameter best reflects selection acting on plant hydraulics is an object for research; in *Picea abies*, there is evidence that tangential diameter provides better biological signal than radial diameter (Rosner *et al.*, 2016; Piermattei *et al.*, 2020). Similarly, given that species differ in how direct or circuitous the route is that water takes within stems (Vité & Rudinsky, 1959; Waisel *et al.*, 1972), even how to measure path length precisely requires examination. Taking tip-to-base conduit diameter widening into account in measurements of plant anatomy and hydraulics – to identify functionally relevant differences for a given height in crucial indices such as hydraulic conductance, leaf specific conductivity, or the Huber value – is therefore an essential area of investigation to move toward study of the conductive system as an integrated whole (McCulloh *et al.*, 2019; Soriano *et al.*, 2020).

IX. Conclusion

Testing hypotheses of the function of tip-to-base conduit widening, and thus its adaptive origin, requires broad collaboration across the wide range of expertise in plant biology. It will require the participation of anatomists, whose insights are essential in the challenging situation of studying conduit diameter across the vast diversity of vascular plants. For example, distinguishing between vessels and conductive imperforate tracheary elements cannot be done based on cell diameter alone or with measurement software (Fig. 5a). Instead, it requires the experience of the trained anatomist, and yet is crucial for accurate measurement of conduit diameters and distributions (Carlquist, 1985b; Barotto *et al.*, 2016; Olson *et al.*, 2020). Similarly, plant physiological expertise will be required to compare the function of the ‘empty zone’ and common variants (Fig. 2), if these can be produced. The expertise of developmental biologists will be required to produce these variants via hormonal or other perturbation (Scarpella, 2017; Johnson *et al.*, 2018), as well as in determining the mechanisms permitting or prohibiting cell expansion along the stem. Testing hypotheses of adaptation also requires the essential participation of all three of the interdisciplinary approaches within evolutionary biology, which are population biology, optimality modeling, and comparative biology (Olson & Arroyo-Santos, 2015). Only broad collaboration across all of these biological disciplines will lead to a satisfactory explanation for the pervasiveness of tip-to-base conduit diameter scaling in the terrestrial vascular plants across extremes of size, life form, and climate world-wide.



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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Table S1 Species providing evidence of predictable tip-to-base conduit widening.

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