

REVIEW AND PERSPECTIVE

# Stretched sapwood, ultra-widening permeability and ditching da Vinci: revising models of plant form and function

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- **Background** The mechanisms leading to dieback and death of trees under drought remain unclear. To gain an understanding of these mechanisms, addressing major empirical gaps regarding tree structure–function relations remains essential.
- **Scope** We give reasons to think that a central factor shaping plant form and function is selection simultaneously favouring constant leaf-specific conductance with height growth and isometric (1:1) scaling between leaf area and the volume of metabolically active sink tissues ('sapwood'). Sapwood volume–leaf area isometry implies that per-leaf area sapwood volumes become transversely narrower with height growth; we call this 'stretching'. Stretching means that selection must favour increases in permeability above and beyond that afforded by tip-to-base conduit widening ("ultra-widening permeability"), via fewer and wider vessels or tracheids with larger pits or larger margo openings. Leaf area–metabolically active sink tissue isometry would mean that it is unlikely that larger trees die during drought because of carbon starvation due to greater sink–source relationships as compared to shorter plants. Instead, an increase in permeability is most plausibly associated with greater risk of embolism, and this seems a more probable explanation of the preferential vulnerability of larger trees to climate change-induced drought. Other implications of selection favouring constant per-leaf area sapwood construction and maintenance costs are departure from the da Vinci rule expectation of similar sapwood areas across branching orders, and that extensive conduit furcation in the stem seems unlikely.
- **Conclusions** Because all these considerations impact the likelihood of vulnerability to hydraulic failure versus carbon starvation, both implicated as key suspects in forest mortality, we suggest that these predictions represent essential priorities for empirical testing.

**Key words:** Adaptation, allometry, forest mortality, sapwood, scaling, xylem.

## INTRODUCTION

Trees are dying by the millions with climate change-induced drought, and despite intense attention from researchers, exactly why remains perplexing (Trugman *et al.*, 2021; McDowell *et al.*, 2022; Fernández-de-Uña *et al.*, 2023). Identifying the most vulnerable species or individuals at a given site, or even developing more drought-resistant varieties, therefore lacks robust guiding theory (Rosner *et al.*, 2021). Such theory is necessary to understand multiple phenomena falling under the broad umbrella of 'forest mortality'. One phenomenon is dieback, in which formerly taller trees shed apical branches and resprout from lower ones, leading to shorter trees (Rood *et al.*, 2000; Davis *et al.*, 2002; Camarero *et al.*, 2015; Fajardo *et al.*, 2019; Gonçalves Andrade Bueno *et al.*, 2020; Anfodillo and Olson, 2021). Another phenomenon is outright mortality, in

which entire individuals die (Allen *et al.*, 2015; Anderegg *et al.*, 2016; Breshears *et al.*, 2018; McDowell *et al.*, 2022). A particularly concerning aspect of mortality is that, on average, the largest individuals seem particularly vulnerable to dying (Bennett *et al.*, 2015; Rowland *et al.*, 2015; Olson *et al.*, 2018; Prendin *et al.*, 2018; Bartholomew *et al.*, 2020). Larger trees sequester disproportionately more carbon and contribute disproportionately more propagules to the next generation than do even slightly smaller trees, so the loss of the largest individuals disproportionately degrades ecosystems (Luyssaert *et al.*, 2008; Lindenmayer, 2017; Vandekerckhove *et al.*, 2018; Enquist *et al.*, 2020). Given the ecological and economic effects of all these phenomena, it is pressingly incumbent on plant scientists to arrive at a consensus regarding the causes of forest mortality.

Numerous authors have rightly pointed out that if amounts of living non-photosynthetic tissue increases per unit leaf area,

then larger individuals will be more vulnerable to mortality under drought because they have larger proportions of sink tissues relative to source tissues (Magnani *et al.*, 2000; Trugman *et al.*, 2018). Under drought conditions, with stomata closed, plants are not replenishing stored carbohydrate reserves, which are continually consumed in respiration. Mortality due to depletion of these reserves is known as carbon starvation (Landhäusser and Lieffers, 2012; Rowland *et al.*, 2015; Gentine *et al.*, 2016). At least since works such as Yoda *et al.* (1965), Kira and Shidei (1967), and Whittaker and Woodwell (1967), many plant biologists have speculated that larger trees could have larger amounts of living sapwood per unit leaf area than smaller individuals (Sala *et al.*, 2011; Hölttä *et al.*, 2013). Larger individuals would therefore be more vulnerable to carbon starvation because they have so much more living sapwood per unit leaf area than smaller individuals. Also, from this perspective, sapwood construction costs, replacement of embolized xylem conduits, osmotic regulation of conductance in conduits or refilling of embolized conduits would all imply greater carbon costs per unit leaf area in a large individual than in a smaller conspecific (Trugman *et al.*, 2018; West, 2020). Based on this, larger individuals are especially vulnerable to drought-induced mortality because of their greater proportion of sink to source tissue. In explaining forest mortality, the view that metabolically active sapwood volume increases per unit leaf area with tree growth therefore focuses attention on carbon starvation and not on other phenomena, such as xylem vulnerability to embolism.

Based on first principles of natural selection, as well as empirical data, we suggest that an increase in sapwood volume per unit leaf area with tree growth is unlikely (Körner, 2012). Instead, it is important to test the notion that natural selection favours an *isometric* (1:1) relationship between metabolically active sapwood volume (note *volume*, as opposed to the more commonly measured sapwood area) and leaf area. Currently, it is often assumed that metabolically active sapwood volume increases per unit leaf area, and authors reason that greater height implies greater conductive pathlength resistance and more marked effects of gravity. More sapwood per unit leaf area would offset these increases in per-leaf area resistance. Under such scenarios with increasing amounts of sapwood per unit leaf area with height growth, the slope of such the sapwood volume–leaf area relationship is greater than 1, and so is described as hyperallometric. An isometric relationship implies a slope of 1, that is that metabolically active sapwood volume keeps pace exactly with leaf area (see Niklas, 1994 for allometry/isometry terminology). If there were such an isometric relationship, it would satisfactorily account for several currently puzzling empirical patterns, which we explore below. We set out a series of predictions that derive from the notion of constant sapwood costs per unit leaf area with height growth. These empirical unknowns describe a landscape of specific predictions that require attention not only for a theory of tree structure and function but also to address ongoing forest mortality.

*The basic premise: selection should favour constant per-leaf area sapwood costs*

It is clear that total shoot mass increases per unit leaf area (Niklas and Enquist, 2001; Enquist and Niklas, 2002; Sillett

*et al.*, 2010, 2015; Mensah *et al.*, 2016). Across trees, shoot mass scales with leaf area with an exponent of  $>1$ , which means that as a tree grows taller, there is increasing total shoot mass per unit leaf area. With continuous accumulation of non-living heartwood, such an increase in total shoot biomass per unit leaf area is inevitable. However, only the living biomass is metabolically active tissue drawing glucose derived from the leaves. The notion that living sink biomass increases per unit leaf area is not only largely untested, but also in contradiction of basic notions of the action of natural selection, which shapes key metabolic scaling relationships (West *et al.*, 1997; Glazier, 2006, 2010).

Natural selection should tend to favour a constant relationship between the amount of living sink tissue and leaf area. Natural selection is the differential survivorship and reproduction of some variants over others within the same species (Olson and Arroyo-Santos, 2015). Living sapwood and phloem together make up a carbon sink, representing both a carbon construction cost as well as the number of mitochondria drawing glucose from the leaves (Ryan *et al.*, 1995). Individuals in which the carbon sink increases per unit leaf area will, as they grow taller, have ever-smaller carbon surpluses directed to further growth and to reproduction. In contrast, in isometric variants, the volume of metabolically active sink tissue remains constant per unit leaf area as a tree grows taller. As a result, instead of surpluses constantly diminishing, isometric variants have constant per-leaf area carbon surpluses that can be directed to further growth and reproduction. With their greater surpluses, isometric variants will grow faster and produce more propagules than variants with increasing sink–source relations, and so come to predominate in populations. By way of comparison, in an individual with sapwood volume–leaf area scaling of 1.3, a 10-fold increase in leaf area would imply a 22-fold increase in sapwood volume. Over the same increase in leaf area, the isometric individual would experience only a 10-fold increase in sapwood volume, exactly keeping pace with leaf area. Given that leaf-specific carbon costs increase by more than double in individuals that experience even a slight increase in sink volume per unit leaf area, it seems more than likely that they are selected against in favour of variants in which sink costs remain constant per unit leaf area.

These expectations predict that selection should therefore favour leaf area–metabolically active sapwood volume isometry. Given that there is some heterogeneity in metabolic rate even between tissues within the same individual (Kutschera and Niklas, 2011, 2013), the broad pattern of sapwood–leaf area isometry almost certainly exhibits some variation about the y-axis, associated with variation in ecological strategy (Fig. 1). For example, the relatively few data available suggest that species with high wood density have higher metabolic rates, consistent with metabolic scaling theory (Poorter and Remkes, 1990; Poorter *et al.*, 1990; Lambers *et al.*, 2008; Castorena *et al.*, 2022). Species with higher density wood should therefore have larger crowns for the same sapwood volume (Iida *et al.*, 2011). By the same token, species with low wood density should have relatively small crowns, but broadly speaking, the main variable predicting metabolically active sapwood volume should be leaf area.

Empirical data are consistent with expectations of leaf area–metabolically active sapwood volume isometry (summarized in Table 1). The few direct measures available regarding leaf

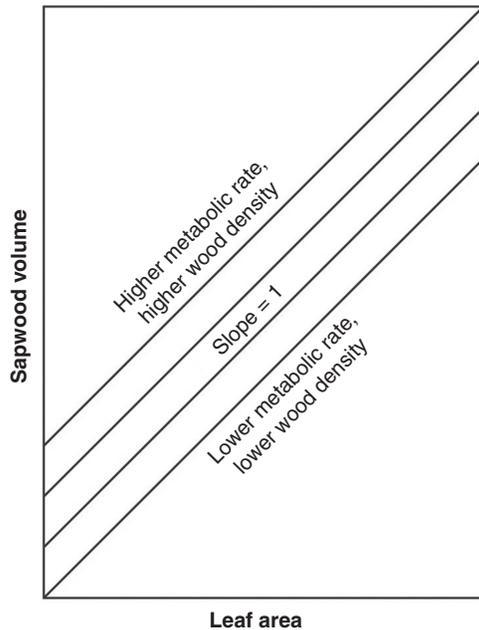


FIG. 1. Across species, metabolically active sapwood volume should scale with leaf area with a slope of 1. Sapwood volume–leaf area isometry characterizes variants within species that maximize growth and reproductive output. There is probably some variation in y-intercept across species associated with ecological strategy. For example, evidence suggests that species with higher wood density have higher metabolic rates per unit xylem volume and more metabolically active sapwood than species with low wood density.

area and sapwood volume, all from conifers, do suggest an isometric relationship [Cermák *et al.*, 1998; together with Urban *et al.*, 2015 (*Pinus sylvestris*); Waring *et al.*, 1980 (*Pseudotsuga menziesii*); Sillett *et al.*, 2010 (*Sequoia sempervirens*)]. Cermák *et al.* (1998) show that needle mass  $M_n$  scales with stem diameter  $D$  as  $M_n \propto D^{1.86}$ . Data from the same trees by Urban *et al.* (2015) show that sapwood volume  $V$  scales as  $V \propto D^{1.9}$ . That these two exponents are practically the same suggests that  $M_n \propto V$ , that is leaf area–sapwood volume isometry. Empirically testing the living sapwood volume–leaf area relationship is thus very much an unexplored frontier. However, complementary data that suggest or are at least congruent with living sapwood volume–leaf area isometry are available. For example, Mori *et al.* (2010) found that respiration scaled isometrically with body mass in small plants. Given that small plants lack heartwood, their non-leaf tissue should be all or mostly living. As a result, respiration should be directly proportional to body mass, and this is the case in Mori *et al.*'s data. In large plants, which have heartwood that contributes non-metabolically active biomass, Mori *et al.* (2010) found that metabolism scaled as the  $\frac{3}{4}$  power of body mass. This finding is consistent with our prediction because we would expect the respiration–body mass slope to decrease as metabolically inactive mass accumulates (Reich *et al.*, 2008; Körner, 2009, 2012). Additional congruent observations are that seed and wood production in trees scale isometrically with leaf mass (Greene and Johnson, 1994; Niklas and Enquist, 2002). If non-photosynthetic carbon sinks diverted increasing amounts of photosynthetic resources per unit leaf area as trees grew larger, then the slope of the

reproductive output–leaf mass relationship would be less than 1, as increasing carbon was diverted to sapwood. Likewise, Petit *et al.* (2023) present intriguing results consistent with sapwood volume–leaf area isometry. They compared the number of sapwood rings between slow-growing and quickly growing temperate ring-bearing trees, finding that for the same leaf area, faster growing plants have fewer but wider active rings, while slower growing ones have higher numbers of narrower rings. Such a tradeoff would seem to require similar sapwood–leaf area relations across individuals. Other authors have documented that non-structural carbohydrate concentrations are similar between small trees and trees at their height limits at a given site (Körner, 2003; Sala *et al.*, 2011). If sapwood carbon cost increased per unit leaf area with height growth, non-structural carbohydrate concentrations would decrease with height growth. Given empirical data and basic principles of natural selection, there is reason to regard the expectation of living sapwood costs remaining constant per unit leaf area with height growth as a prediction in serious need of empirical testing. We now highlight this need by exploring some of the correlates of this basic premise.

#### Premises for a theory of tree form, function and mortality

If selection favours constant per-leaf area carbon sink costs, then a series of expectations regarding trait covariation are implied. Most of these remain virtually untested, but because they are at least plausible, and all have at least some empirical data compatible with them, they help identify important gaps in scientific knowledge regarding plant form and function that require testing if plant scientists are to build a solid understanding of forest mortality. We explore 15 of these here.

#### Hydraulic resistance is independent of tree height

Within species, selection should favour variants in which leaf-specific photosynthetic productivity remains constant as an individual grows taller. Within a population of a species, individuals in which photosynthetic productivity per unit leaf area decreases with height growth will have less and less carbon surplus per unit leaf area that can be directed to reproduction and to growth. Individuals in which leaf-specific productivity remains constant with height growth will have consistently higher carbon surpluses per unit leaf area. Higher carbon surpluses per unit leaf area mean greater amounts of carbon invested in further growth and in reproduction. Therefore, individuals that maintain constant leaf-specific productivity with height growth will have higher fitness than conspecifics in which it decreases. Selection will therefore push as far as possible toward constant leaf-specific photosynthetic productivity with height growth in all species. Within any given species, a given rate of leaf metabolism is broadly associated with a given rate of water consumption (Scoffoni *et al.*, 2016). As a result, selection should favour conductance that remains constant per unit leaf area as a tree grows taller.

Height growth implies longer and longer root-to-leaf transport distances. Tubes that are longer have more wall area intervening between roots and leaves, meaning more friction and thus greater hydraulic resistance and reduced conductance (Vogel, 2003). If conductive pathlength increases without any

TABLE 1. Empirical observations that suggest sapwood volume–leaf area isometry

Observation	Why it suggests sapwood–leaf area isometry	References
Reports of isometric sapwood volume–leaf area	While data are scant and include sapwood delimited by eye, rather than determining metabolically or conductively active volume, some available information suggests isometry	(Cermák <i>et al.</i> , 1998; Sillett <i>et al.</i> , 2010; Urban <i>et al.</i> , 2015)
Isometric scaling of biomass with leaf area in small plants, decreasing in larger ones	Small plants should have mostly living non-leaf tissue, and so non-leaf–leaf biomass scaling should be isometric. If living sapwood volume–leaf area scaling remains isometric with height growth, then the leaf area–total biomass scaling exponent should be less than one in large plants because of the accumulation of non-metabolically active heartwood	(Vanninen <i>et al.</i> , 1996; Niklas and Enquist, 2001; Mori <i>et al.</i> , 2010)
Decrease in sapwood area per unit leaf area with height growth (‘stretching’)	Available empirical data show that per-leaf area sapwood area at comparable points along shoots decreases per unit leaf area from short to tall plants of the same species	(Cermák and Nadezhdina, 1998; Mokany <i>et al.</i> , 2003; Koch <i>et al.</i> , 2015; Sillett <i>et al.</i> , 2015; Urban <i>et al.</i> , 2015)
Increase in vessel diameter at shoot tip with plant height in angiosperms	Increase in vessel diameter at the shoot tip with plant height reduces per-vessel resistance, meaning that fewer vessels per unit transectional area can supply the same leaf area as a plant grows taller. Fewer conduits per unit leaf area in taller plants would contribute to maintaining carbon costs constant per unit leaf area. If sapwood volume were free to proliferate per unit leaf area with plant height, constant leaf-specific conductance could be achieved by simply adding more and more vessels of the same tip diameters per leaf area with height growth. It is unclear why vessel diameter at the tip would increase with height unless selection maintains sapwood volume constant per unit leaf area	(Olson <i>et al.</i> , 2014, 2018, 2021; Echeverría <i>et al.</i> , 2019)
Constant biomass production across species differing in height	If sapwood volume increased per unit leaf area with height growth, then leaf-specific biomass production would decrease with height growth because of decreasing per-leaf area carbon surpluses resulting from more and more carbon diverted to ever-increasing sink tissues	(Waring <i>et al.</i> , 1980; Sillett <i>et al.</i> , 2010)
Constant reproductive output per unit leaf area with height growth	If non-photosynthetic carbon sinks diverted increasing amounts of photosynthetic resources per unit leaf area as trees grew larger, then the slope of the reproductive output–leaf mass relationship would be less than one, as more and more carbon was diverted to sapwood	(Niklas and Enquist, 2002; Greene and Johnson, 2004)
Departure from packing limit expectations: increase in vessels per mm <sup>2</sup> xylem transectional area with height growth (as at the stem base)	As a tree grows taller, per-vessel carbon costs increase because conductive pathlength is longer. Deviation of carbon from other xylem cell types to vessels as sapwood volumes ‘stretch’ would plausibly contribute to maintaining constant sapwood volume–leaf area carbon costs	(Olson <i>et al.</i> , 2014)

other attendant changes (e.g. conduit diameter remains constant), then conductance will drop predictably with an increase in height (Gentine *et al.*, 2016; Trugman *et al.*, 2018). However, conduits do not remain of constant diameter, instead widening tip-to-base. This tip-to-base widening occurs such that resistance accumulates much more slowly than it would if conduits were of constant diameter (Becker *et al.*, 2000; Petit and Anfodillo, 2009; Savage *et al.*, 2010; Olson *et al.*, 2021). Across terrestrial vascular plants, conduits are narrow at the stem tips, widening quickly from the stem tip toward the base. After the first 30 cm or so of distance from twig tips, the widening rate quickly becomes lower, meaning that conduit diameters increase slowly along most of the conductive path. Because conductance scales as the fourth power of conduit diameter, but resistance only increases linearly with conduit length, these small increases in conduit diameter markedly offset the accumulation of resistance due to increasing pathlength (West *et al.*, 1999; Becker *et al.*, 2000; Anfodillo *et al.*, 2006; Petit and Anfodillo, 2009; Koçillari *et al.*, 2021; Olson *et al.*, 2021). Widening is not so great, however, as to lead to unnecessary increases in vulnerability to embolism or excessive carbon costs (Koçillari *et al.*, 2021). This pattern of within-individual tip-to-base conduit widening gives rise to a correlation across species between conduit diameter and plant height (Anfodillo *et al.*, 2006; Zach *et al.*, 2010; Olson *et al.*, 2018, 2020, 2021; Zhong *et al.*, 2019, 2020; Levionnois *et al.*, 2021).

Tip-to-base conduit widening, together with probable increases in per-sapwood area permeability that we discuss below, make it plausible that leaf-specific conductance remains constant as a tree grows from sapling to tall adult (Petit *et al.*, 2008; Sterck *et al.*, 2012; Yang *et al.*, 2021). The observation that plants fix similar amounts of carbon per unit leaf area across species independent of height (Poorter *et al.*, 1990; Selaya & Anten, 2010; Stephenson *et al.*, 2014; Michaletz *et al.*, 2014; Castorena *et al.*, 2022; see also Sillett *et al.*, 2010; Echeverría *et al.*, 2019) seems hard to account for unless trees somehow maintain flow to leaves with height growth [we say ‘constant’ throughout, but S. Gleason (pers. comm.) has pointed out that ‘at least constant’ might be more correct, if an increase in height locates leaves in higher vapour pressure deficit situations, leading to greater conductance per unit leaf area with height growth, see e.g. (Olson *et al.*, 2020)]. There is thus compelling theory and empirical evidence that leaf-specific conductance is independent of pathlength. As a result, from the point of view of hydraulic resistance, there are reasons to think that it is unnecessary to posit increases in sapwood per unit leaf area.

#### ‘Stretching’ of per-leaf area living sapwood volume

As we argue above, instead of selection favouring an increase in living sapwood volume per unit leaf area with tree

height growth, it should instead favour a constant relationship. We mention ‘shoot living sapwood’ as a shorthand but this includes all the non-photosynthetic sink tissues, such as the roots and non-photosynthetic living tissue in the bark, both of which are discussed in more detail below. Presumably selection favours constancy per unit leaf area in all sapwood carbon costs – construction, growth metabolism, maintenance metabolism – though this expectation remains largely open for study (see, for example, Ryan *et al.*, 1995; Lambers *et al.*, 2008; Chapin *et al.*, 2011). For the purposes of simplicity, we focus here on living sapwood in the shoot, to facilitate explaining a key point.

This key point is what we have referred to as the ‘stretching’ of per-leaf area sapwood volume (Olson *et al.*, 2014). Given ‘stretching’, sapwood [the secondary xylem includes vessels if present plus rays, axial parenchyma and imperforate tracheary elements; see Olson (2023)] volume per unit leaf area remains constant per unit leaf area as a tree grows taller. The total amount of sapwood can be thought of as a series of volumes, each corresponding to a given unit of leaf area. Because a given unit of leaf area is supplied by conduits in series that stretch from the base to the tip, these per-leaf area volumes of sapwood are also continuous tip-to-base (as in Fig. 2). In any geometric figure of constant volume, lengthening any one side inevitably implies a reduction of the others. Trees are no exception. A taller individual must necessarily have narrower living leaf-specific sapwood cross-section at any point of the shoot as compared to a shorter conspecific of the same total sapwood volume and leaf area (Fig. 2).

Empirical evidence is consistent with the expectation of ‘stretched’ sapwood. For one, empirical measures of the sapwood area–leaf area relationship across conspecifics of differing sizes tend to reveal slopes below 1. Sapwood area ( $A_S$ )–leaf area ( $A_L$ ) slopes  $<1$  indicate that, as individual trees grow taller, sapwood cross-sectional area becomes smaller per unit leaf area, as predicted given ‘stretching’. Because for the same leaf area sapwood area widens tip-to-base along a plant stem (Soriano *et al.*, 2020), data would ideally examine comparable parts of the shoot, such as at the shoot base or known distances from the stem tip. Some such studies include data from *Pinus sylvestris* by Cermák *et al.* (1998), who, together with the data of Urban *et al.* (2015), suggest  $A_S \propto A_L^{0.88}$ . In *Sequoia sempervirens*, Sillett *et al.* (2015) suggest  $A_S \propto A_L^{0.87}$ . Data on the small angiosperm tree *Ricinus communis* (Berry *et al.*, 2024), based on measurements of sapwood volume using triphenyltetrazolium staining (Ruf and Brunner, 2003), show scaling in a similar neighbourhood, with  $A_S \propto A_L^{0.6}$ . Studies from two species of *Eucalyptus* and one species of *Quercus* all show that the leaf area–sapwood area relationship increases with plant height (Mokany *et al.*, 2003; Phillips *et al.*, 2003; Koch *et al.*, 2015), again consistent with ‘stretching’.

Testing the metabolically active sapwood volume–leaf area relationship emerges as an important priority given the numerous potential repercussions of ‘stretching’. Traditionally, sapwood is distinguished from heartwood using characteristics such as colour, moisture content or translucency (Quiñonez-Piñón and Valeo, 2018). Estimating sapwood area or volume on the basis of these measurements assumes that metabolic activity is distributed uniformly throughout the sapwood. However, the distribution of metabolically active cells in

sapwood is highly heterogeneous (Ebermann and Stich, 1985; Cermák and Nadezhdina, 1998; Pruyn *et al.*, 2002; Chapotin *et al.*, 2006; Spicer and Holbrook, 2007; Makita *et al.*, 2012; Berry *et al.*, 2023). In broad terms, metabolic activity often is highest near the cambium and declines toward the centre. However, the few studies that have been done, for example using triphenyltetrazolium staining, which identifies cells with mitochondrial activity (Ruf and Brunner, 2003), (Castorena, 2016) suggest that metabolic activity is often distributed in tangential bands or, commonly, around vessels, in ways that are not predictable based on traditional criteria for delimiting sapwood (Castorena, 2016; Berry *et al.*, 2024). As a result, traditional measures of sapwood area seem certain to overestimate the true extent of metabolically active sapwood (cf. Wells and Eissenstat, 2002). This overestimation will reinforce the idea that sapwood increases per unit leaf area rather than remaining constant. It is therefore worth exploring the possibility that studies that do report increases in sapwood area per unit leaf area with height growth (e.g. McDowell *et al.*, 2002) overrepresent the amount of metabolically active sapwood because of traditional measurement techniques.

#### *Ultra-widening permeability with height growth: the root–shoot system*

Living sapwood ‘stretching’, plus the fact that tip-to-base conduit widening does not entirely compensate for increases in resistance with height growth, mean that factors beyond widening must contribute to decreases in resistance with height growth. We designate these decreases in resistance as ‘ultra-widening’ permeability because they are beyond the increases in conductance conferred by widening alone (Fig. 3). ‘Stretching’ means that, as a tree grows taller, the transverse area of living sapwood supplying the same leaf area diminishes. Such ‘stretching’ should lead to concurrent adaptations that maintain per-leaf area conductance constant with height growth as transverse xylem area diminishes. These adaptations should lead to increases in permeability (greater conductance given the same pressure differential) for a given xylem cross-sectional area (Fig. 2). Such increases have been documented in studies that examine permeability at comparable points (e.g. the trunk base) on conspecifics of different heights in conifers (Domec and Gartner, 2003; Domec *et al.*, 2012) and in angiosperms (Mokany *et al.*, 2003). In *Eucalyptus regnans* trees ranging from 60 to 90 m tall, Koch *et al.* (2015) report that stomatal conductance remains constant, but sapwood area per unit leaf area at the crown base declines dramatically. These observations are exactly in line with what we predict here, and what models such as the West, Brown and Enquist model of plant function (West *et al.*, 1999) predict: selection should favour constant conductance per unit leaf area. However, in contrast to existing models, we suggest that this constant conductance must occur through ever-decreasing xylem transverse areas with height growth. Such constancy through diminishing area would necessarily seem to require an increase in permeability with height growth. Such increases in per-xylem area permeability at the trunk base are expected because taller plants have wider conduits, which conduct more water for the same conductive pathlength.

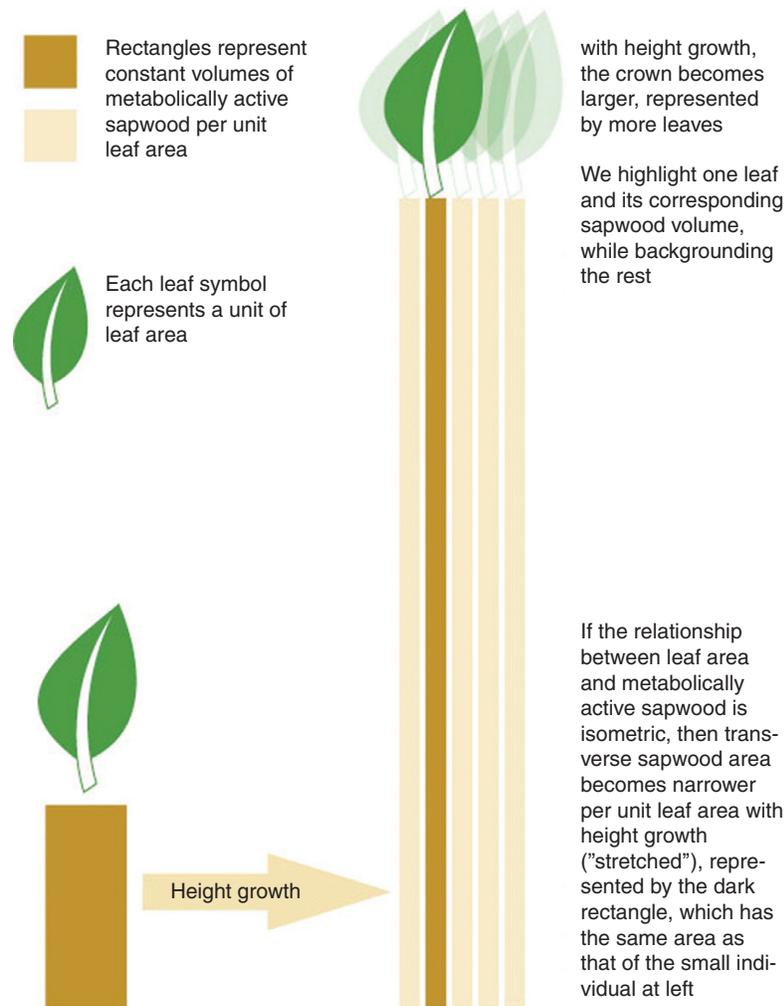


FIG. 2. Here, we represent our prediction of the ‘stretching’ of per-leaf area sapwood transverse area. Given metabolically active sapwood volume–leaf area isometry, as a tree grows taller, metabolically active sapwood per unit leaf area necessarily becomes transversely narrower. This narrowing means that there is less transverse xylem area that must supply a given unit leaf area as an individual grows taller.

What remains to be seen is whether permeability increases more than expected given conduit widening with plant height, which is what we predict here. Ideally, measurements should be made at similar distances from the stem tip (say 10 cm) between tall and short conspecifics (Fig. 4). Measuring at the same distance from the tip takes into account the predictable pattern of tip-to-base conduit widening observed along the stems of terrestrial vascular plants, and as we explain below, taking including leaf size as a covariable takes into account widening in the leaf. If permeability increases with height, then taller plants should show higher permeability than shorter conspecifics even when examining samples taken from the same distance from the shoot tip and in conduits of the same diameters and lengths.

Various structural mechanisms could lead to ultra-widening permeability with height growth in the root–shoot system. One mechanism, which has been observed in vessel-bearing angiosperms, involves changes in conduit diameter and number with height growth (Echeverría *et al.*, 2019). Given a constant rate of tip-to-base conduit widening, conduits with wider apical

diameters are wider along their entire lengths. Because conductance scales as the fourth power of conduit diameter, conduits wider along their entire lengths conduct considerably more water than conduits even slightly narrower (Ewers, 1985; Ewers *et al.*, 2007). As transverse xylem area diminishes, selection could favour fewer, apically wider conduits per unit leaf area (Fig. 4). A reduction in conduit number would contribute to keeping xylem construction costs per unit leaf area constant with height growth. Such a scenario would explain observed data of reduction in conduit number per unit leaf area with height growth within species (Echeverría *et al.*, 2019) and the observed pattern of increase with plant height in vessel diameter at the stem tip across angiosperm species (Zach *et al.*, 2010; Olson *et al.*, 2014, 2018; see also the data of Koçillari *et al.*, 2021). Across species, taller vessel-bearing angiosperms tend to have predictably wider vessels at the stem tip (1 cm from the shoot apex). Small increases in shoot apex conduit diameter (the ‘starting diameter’ for vessel widening in the shoot–root system) would lead to very marked increases in permeability, rivalling or exceeding tip-to-base conduit widening in their

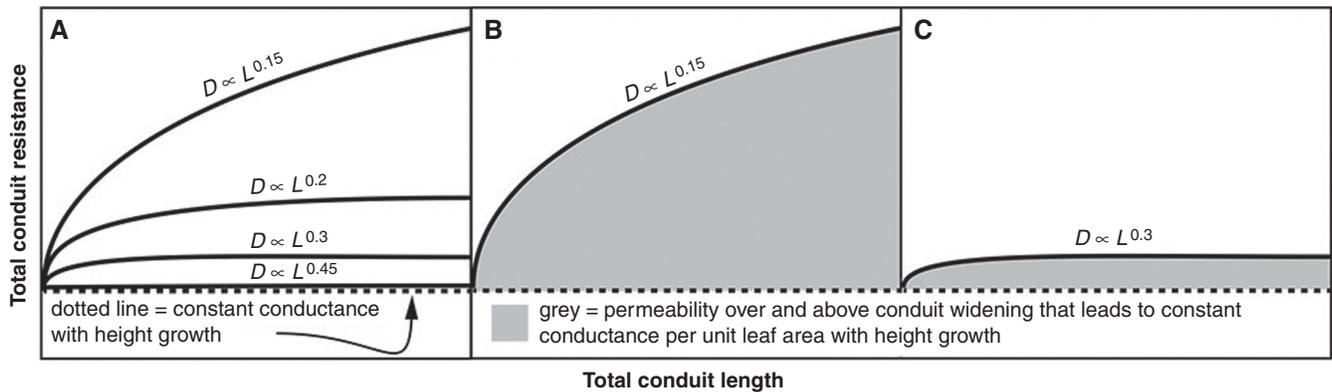


FIG. 3. Ultra-widening permeability in the secondary xylem. (A) As conductive pathlength increases, hydraulic resistance accrues and conductance decreases. The rate of tip-to-base conduit widening is given by the exponent of the relationship between conduit diameter  $D$  and conductive pathlength  $L$ . A widening exponent  $w$  of 0.15 describes conduits that widen relatively little tip-to-base, with substantial accumulation of resistance. A  $w$  of 0.45 is enough to keep resistance, and thus whole-plant conductance  $G_t$ , essentially constant, with  $G_t \propto L^{-0.02}$  (the dotted line represents constant leaf-specific conductance with height growth). Such high exponents have so far only been observed in leaves. Stems, which account for less than 15 % of total pathlength resistance, have exponents of 0.1–0.3, not sufficient to maintain leaf-specific conductance constant. For example, when  $w = 0.07$ ,  $G_t \propto L^{-0.65}$ . Therefore, if conductance does remain constant per unit leaf area, some increase in permeability additional to tip-to-base conduit widening must be at work. (B, C) This permeability above and beyond widening is ‘ultra-widening permeability’. Ultra-widening permeability should be inversely proportional to the widening exponent. (B) The grey field highlights the difference between constant conductance (dashed line) and the resistance that accumulates with the relatively low exponent of 0.15. (C) A higher rate of widening means that less ultra-widening permeability is needed in reaching constant conductance. It thus seems possible that there is an inverse relationship between the rate of tip-to-base conduit widening and ultra-widening permeability.

importance in altering tissue-level permeability. We are not aware of any other hypothesis, other than selection favouring an increase in permeability per unit xylem transectional area in the context of ‘stretching’, that explains the scaling of angiosperm shoot apex vessel diameter with height (Zach *et al.*, 2010; Olson *et al.*, 2014, 2018).

Alterations in inter-conduit pit membrane features represent another mechanism that could lead to increased permeability with height growth. In *Acer*, the data of Lens *et al.* (2011) show that xylem-specific conductivity was strongly negatively predicted by inter-vessel pit membrane thickness (slope =  $-0.77$ ,  $R^2 = 0.69$ ), as did Isasa *et al.* (2023) across 20 species of temperate angiosperms (slope =  $-0.61$ ,  $R^2 = 0.14$ ) (see also Pfautsch *et al.*, 2018). Likewise, Plavcová *et al.* (2011) found that shaded poplars, which were on average taller, had thinner inter-vessel pit membranes as compared to sun-grown, shorter ones. These data suggest that in angiosperms, thinner inter-vessel pit membranes at comparable points on the stem between tall and short individuals could lead to increases in permeability. This possibility predicts that at comparable distances from the shoot tip (say 10 cm), and taking leaf size into account, a tall plant could have thinner inter-vessel pit membranes for a given vessel diameter than shorter conspecifics (Li *et al.*, 2023). Greater total pit membrane area per vessel could also lead to increased permeability given the right patterns of conduit–conduit contact (Choat *et al.*, 2008).

In torus-margo-bearing conifers, tracheids at similar points in the stem could also differ in permeability between tall and short plants. For example, at the same distance from the tip, say 10 cm, tracheids could be of similar dimensions but have larger pits or pits with larger margo openings than those at the same distance from the tip in small plants (cf. Lazzarin *et al.*, 2016) (Fig. 4). Data from comparable distances from the stem tip across plants of differing heights, as in the treetop samples of Domec *et al.* (2008), are essential because tip-to-base conduit

widening means that samples even from slightly differing points along the same stem can have very different conduit dimensions (Olson *et al.*, 2021). The most rigorous test of these possibilities would therefore be to compare tracheids of similar dimensions, from similar distances from the stem tip, in trees of differing heights, controlling for leaf size (see below). The accumulation in resistance of the secondary xylem system is rapid over the first 3 m or so of height growth, becoming more gradual as the tree becomes larger. As a result, comparisons would ideally compare saplings well below 3 m with large trees.

#### Ultra-widening permeability with height growth: leaves

In addition to plausible sources of ultra-widening permeability in the root–shoot system, it also seems possible that increases in permeability could be due to alterations in leaves, including the extra-xylary pathway. Leaves typically account for less than 1 % of the total conductive pathlength, but their contribution to total conductive pathlength resistance is substantial. Total pathlength hydraulic resistance is the sum of four sequential resistances, roots, shoots, leaves and the extra-xylary pathway within the leaf (Lechthaler *et al.*, 2020; Scoffoni *et al.*, 2023). Xylem conduits within leaves are much narrower compared to the rest of the path (e.g. terminal conduits are often less than 5  $\mu\text{m}$  in diameter, whereas diameters in the stem and roots can be tens or hundreds of micrometres). Tip-to-base conduit widening plays a pivotal role in the accumulation of resistance toward the treetop and in particular within the leaves. As a result, variation in leaf resistance with height growth is another locus that needs exploring to test the expectation of ultra-widening permeability increases.

Slight increases in tip-to-base conduit widening rates in leaves with height growth constitute one possible source of ultra-widening permeability increase. Under such a scenario,

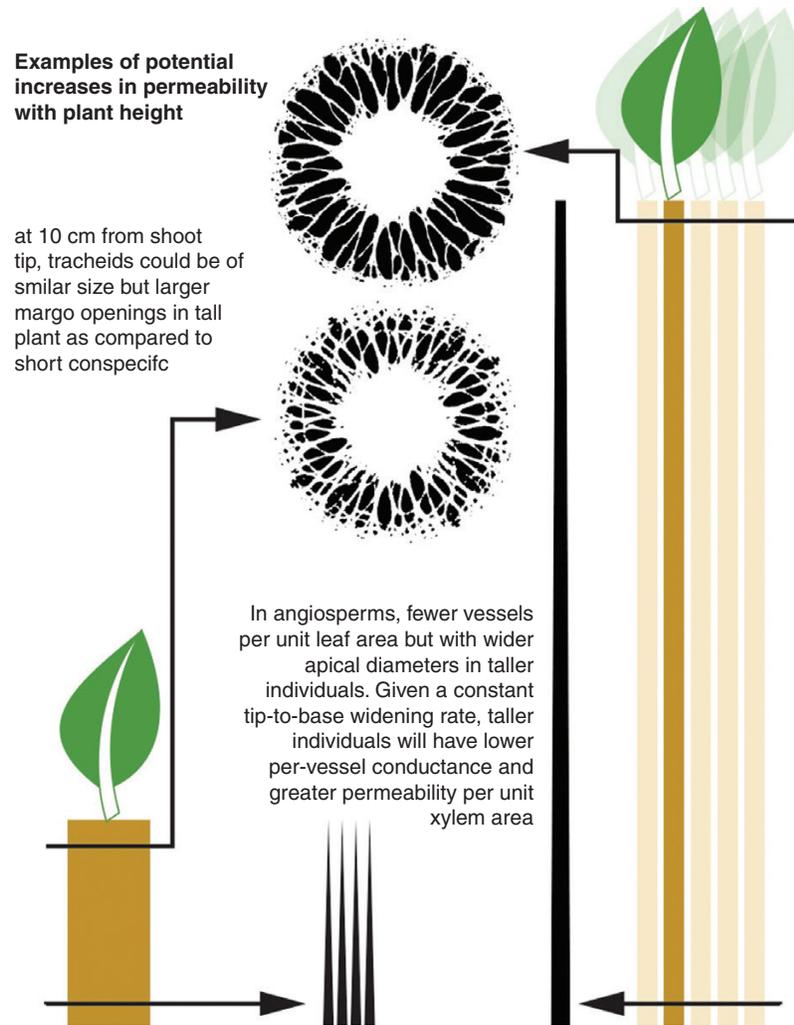


FIG. 4. ‘Stretching’ and increase in permeability with height. Using similar conventions as Fig. 2, this figure illustrates examples of possible mechanisms of ultra-widening permeability. Given ‘stretching’, because the transectional xylem area supplying a given unit of leaf area diminishes as an individual grows taller, selection maintaining conductance constant per unit leaf area plausibly leads to increases in xylem permeability of the base-to-tip conductive path. We illustrate two possible mechanisms here. In torus-margo-bearing conifers, tracheids in taller plants could have larger margo openings than smaller individuals of the same species. Because conduits widen predictably tip-to-base along stems, and because pit characteristics scale predictably with tracheid length and diameter tip-to-base (Lazzarin *et al.*, 2016), it is necessary to compare tracheids from the same distance from the stem tip (we give the example of 10 cm from the tip here), or at least take pit dimension scaling with tracheid size into account. In angiosperms, there is evidence that terminal twig vessel diameters increase with plant height (Echeverría *et al.*, 2019; Olson *et al.*, 2021). Given a constant rate of tip-to-base conduit widening, conduits that are wider at the stem tip (and therefore along their entire lengths) will have markedly lower resistance than ones that are narrower at the tip, because conductance scales as the fourth power of conduit radius. Both of these mechanisms could plausibly contribute to greater permeability of the base-to-tip conductive path in taller plants as compared to shorter conspecifics.

as a tree gets taller, leaves would have wider mean petiole base conduit diameters given leaf length at comparable points, as at the treetop, as compared to shorter conspecifics. Given the very marked tip-to-base rate of conduit widening in angiosperm leaves, this mechanism seems likeliest to occur, if at all, in angiosperms. In angiosperm leaves, xylem conduit diameter scales with distance from the leaf tip typically with exponent around 0.5, that is, about twice as fast as widening in stems. Higher tip-to-base conduit widening rates in leaves of taller individuals would mean that for the same pathlength, leaves would oppose less resistance than similar-sized leaves in shorter conspecifics.

In contrast, conifers studied to date appear to have much less marked rates of tip-to-base conduit widening in their leaves

(Lechthaler *et al.*, 2020). As a result, in conifers, a possible source of lowered resistance with height growth is simply alteration in leaf length with height, as occurs in coast redwoods (*Sequoia sempervirens*) (Koch *et al.*, 2004; Oldham *et al.*, 2010; Chin *et al.*, 2022). At the bases of tall redwoods, leaves are relatively long, with wide laminae. At the treetops, however, they are tiny and scale-like. Some authors have explained this gradient in leaf size as the inevitable result of turgor decreases with height, imposed by gravity and conductive pathlength resistance. Their hypothesis is that larger leaves would be favoured by selection at the treetop, but that these are developmentally impossible because trees cannot muster the requisite turgor at the treetops sufficient for greater leaf expansion (Koch *et al.*, 2004; Woodruff *et al.*, 2004; Woodruff and Meinzer, 2011;

Zhang *et al.*, 2012). This scenario seems unlikely, because it predicts that the distribution of traits such as leaf length or leaf cell size should be very narrow on the left side (shorter leaves) and abruptly curtailed on the right, where the turgor-imposed limit of leaf length occurs (see Segovia-Rivas and Olson, 2023 for detailed reasoning). As a result, the base-to-treetop decrease in leaf size in species such as *Sequoia* remains difficult to explain. Ultra-widening permeability increase could account for this gradient. The hydraulic resistance imposed by gravity and that not compensated for by tip-to-base conduit widening (Fig. 3) could be ameliorated by a decrease in leaf length. If tip-to-base widening is relatively mild, then Poiseuille’s law (Tyree and Ewers, 1991; Vogel, 1994) shows that resistance decreases essentially linearly with tube length. The tiny, scale-like leaves at the tops of tall redwoods have very short conductive pathlengths compared to leaves lower in the crown, plausibly contributing to ultra-widening permeability increases that maintain conductance to the leaves despite very large increases in height growth.

An example will illustrate the potential contribution of alterations in leaf length to ultra-widening permeability in conifers. Assume a conifer with a widening rate of conduit diameter  $D$  with length of the conductive path (distance from the leaf tip)  $L$  of  $D \propto L^{0.2}$ . Assume that total pathlength resistance of an individual with leaves 4 cm long is equal to 100. Assume also that the leaf conduits contribute 80 % of the total pathlength resistance, an empirically realistic figure (Lechthaler *et al.*, 2020). Now assume an individual that is identical except that instead of having leaves 4 cm long, the leaves are 1 cm long. The total pathlength resistance relative to the plant with 4-cm leaves is just 60 (Fig. 5), a stunning lowering of total xylem pathlength resistance given very small alterations in leaf length. This example illustrates not only the plausible participation of alterations in leaf length in ultra-widening permeability, but also provides a more likely explanation for the changes in leaf length with height in conifers such as *Sequoia* than alternative hypotheses such as turgor limitation (Koch *et al.*, 2004; Segovia-Rivas and Olson, 2023).

The extra-xylary pathway also provides potential sources of ultra-widening permeability. The passage of water from the xylem to the stomata (via the extra-xylary pathway) encounters resistance roughly equivalent to the entire leaf’s resistance (Nardini *et al.*, 2005; Sack and Holbrook, 2006). Given the contribution of leaves to total pathlength resistance, it seems plausible that even small decreases in features such as bundle sheath resistance could lead to marked increases in ultra-widening permeability (Scoffoni *et al.*, 2023). Recognizing the pivotal role of leaves in determining an entire tree’s hydraulic resistance is essential when assessing the impact of various vascular system features in stems and branches, including ultra-widening permeability. For instance, with a basipetal widening rate of 0.2, the relative increase in hydraulic resistance as a plant grows from a 1-m-tall sapling to a 100-m-tall tree is ~3-fold. Therefore, if the stem’s contribution accounts for 5 % of the total resistance in a small plant, this implies that height growth results only in a maximum increase of 10 % in total resistance from 1 to 100 m. The rest must be accounted for by the leaves. Whatever the source of ultra-widening permeability, there should be an intricate coordination with increasing plant height, as transverse xylem area and features such as conduit number diminish

per unit leaf area, and conduit diameter increases in such a way that carbon costs and conductance remain constant per unit leaf area.

*Constant number of conduits per unit leaf area between conspecifics of the same height*

Given similar demand for water per unit leaf area, and similar conduit characteristics between the individuals of a species, there should be a more or less constant number of conduits per unit leaf area between individuals of the same height (Fig. 6). As in the Pipe Model, similar numbers of conduits per unit leaf area mean that conspecifics of the same height should show isometric scaling between leaf area and conduit number (Shinozaki *et al.*, 1964a, b; Tyree and Ewers, 1991). Because plant height is the main driver of variation in conduit diameter (Olson *et al.*, 2018), conspecifics of the same height should have conduits of the same mean diameters at comparable points on the stem (as at the stem base) even though they have differing leaf areas (Fig. 6). Across individuals of the same species of the same height, individuals with larger crowns and greater leaf area should have larger numbers of water-conducting conduits. They also should have proportionally greater living sapwood volumes. Therefore, a tree with higher leaf area should have a thicker trunk than a conspecific of similar height but lower total leaf area (Tyree and Ewers, 1991), and both should have conduits of similar diameters at comparable distances from the stem tip. We have dubbed this combination of similar numbers of conduits per unit leaf area plus conduit widening the ‘Widened Pipe Model’ (Rosell and Olson, 2019; Koçillari *et al.*, 2021).

*Constant number of conduits per unit leaf along the trunk of a single individual: no ‘furcation’*

According to a Widened Pipe Model, conduit number should be constant per unit leaf area not only between individuals of the same height and species but also tip-to-base along the trunks of individual trees. The potential for tip-to-base conduit widening plus ultra-widening permeability (Fig. 4) to maintain per-leaf area water supply constant means that there is no need to postulate proliferation in the number of conduits per unit leaf area as one moves from the base of a tree toward the tip, a phenomenon known in the literature as ‘furcation’. In animal conductive systems, a single aorta departs the heart. It soon branches, and these daughter arteries themselves branch. This furcation continues until reaching the distal end of the conductive stream, the capillaries. The relationship between mother and daughter branches is such that fluid flow remains constant at each level of the network (Vogel, 1994). As compared to a situation in which each capillary leads independently to the heart, animal circulatory systems in which conduits coalesce proximally cost much less in terms of construction.

Within the trunk of a tree, however, furcated transport networks would be very costly and so are not favoured by selection (Fig. 7). Selection favours high ‘redundancy’ in wood conduit networks, understood as a sufficiently high number of conduits per unit leaf area so that plants can sustain extensive damage and retain conductance to leaves (Carlquist, 1966; Ewers *et*

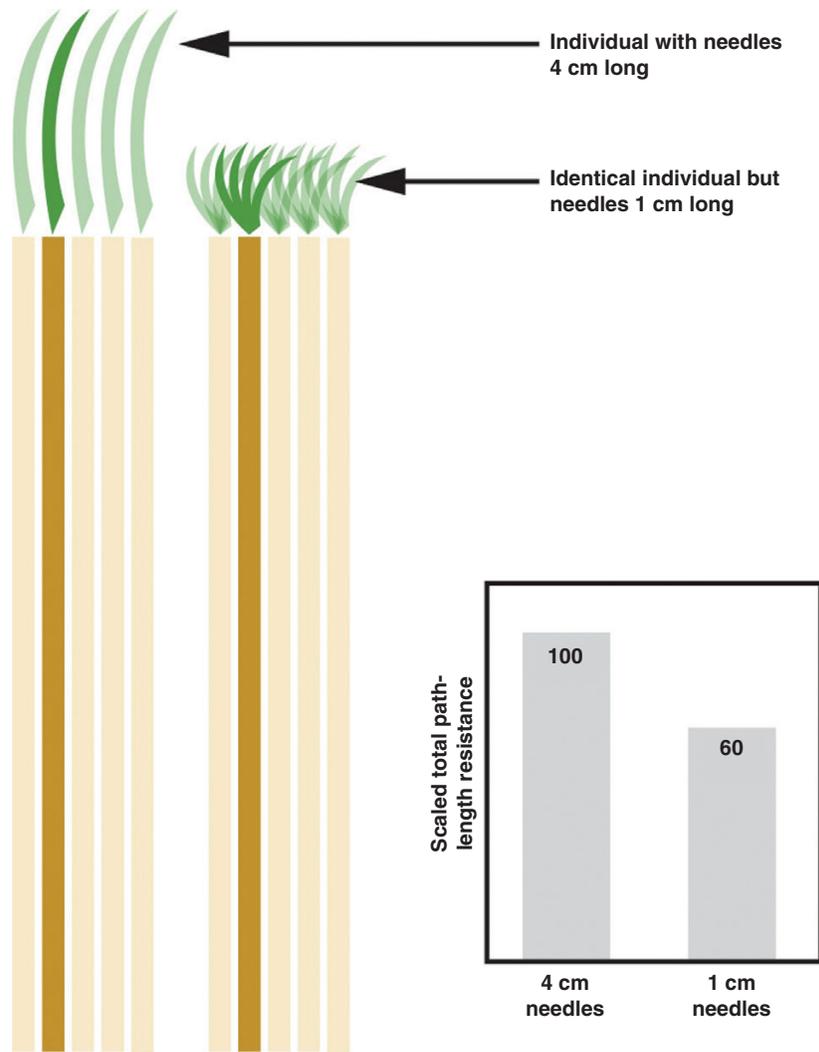


FIG. 5. Reduction of leaf length potentially leads to dramatic ultra-widening permeability. Tip-to-base conduit widening rates in angiosperms are typically quite high,  $>0.4$ , but seem to be lower in conifers, around 0.2 in the data available. If so, then small changes in leaf length in conifers should lead to dramatic changes in total pathlength resistance. Most of the total xylem resistance is concentrated in the leaves, with 80 % being a realistic generalization. The less conduits widen tip-to-base (the more tube-like they are), the greater the importance of changes in pathlength on total resistance. Assuming a tip-to-base conduit widening rate in the leaves of 0.2, two conifer trees of the same height, one with needles 4 cm long and one with needles 1 cm, will have markedly different total pathlength resistances. Scaling the total pathlength resistance of the 4-cm leaf individual to 100, then the total pathlength resistance of the 1-cm needle individual is a dramatically lower at 60. We have drawn the 1-cm leaf plant with four leaves per unit sapwood volume simply to depict a similar leaf area–sapwood volume relationship in both individuals. How a similar leaf area–sapwood volume relationship might be achieved in the presence of leaf shortening with height growth remains to be determined. The various unknowns notwithstanding, changes in leaf length seem a probable source of ultra-widening permeability, and a plausible explanation for changes in leaf length with height in conifers such as *Sequoia*.

*al.*, 2007, 2023; Dietrich *et al.*, 2018). As a result, in contrast to animal circulatory systems, in which there is a single artery proximally, at proximal positions such as at the stem base, in plants there are thousands of conduits. Assume two trees of the same height, same leaf area and the same number of conduits at the base. One individual has a constant number of conduits tip-to-base, which widen following the conventional pattern that maintains conductance per leaf area constant (Petit *et al.*, 2023). The other individual has a ‘furcated’ conductive system (Rosell and Olson, 2019). In the ‘furcated’ individual, the number of conduits increases constantly at each branching level, such that as compared to the base there are vastly more conduits at the stem tip (as in the models of Savage *et al.*, 2010; Sperry *et al.*,

2012; von Allmen *et al.*, 2012; Hölttä *et al.*, 2013). This ‘furcated’ system, with its vastly higher number of conduits for the same leaf area, would also cost much more in terms of carbon than the system with a fixed number of conduits tip-to-base. There is every reason to expect that selection should favour variants with lower per-leaf area carbon cost. It is clear that conductive systems in leaves furcate abundantly, especially toward the distalmost ends of the conductive system (McCulloh *et al.*, 2003, 2009; Gleason *et al.*, 2018; Lechthaler *et al.*, 2019). There is much less evidence in stems, and the evidence available suggests that conduits furcate little or only in the apicalmost portions of the root–shoot system (McCulloh *et al.*, 2003, 2004; Atala and Lusk, 2008; Petit *et al.*, 2008). As a result, it

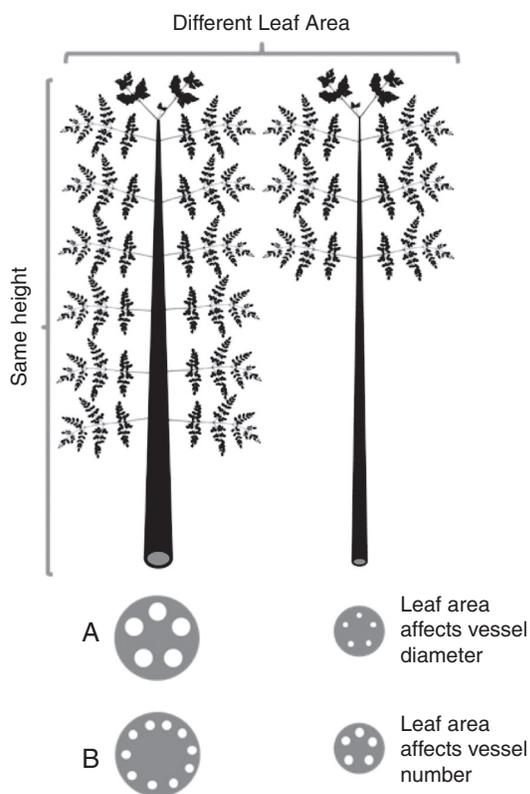


FIG. 6. Given tip-to-base conduit widening, conspecifics of similar height have similar mean conduit diameters at comparable points on their shoots (as at the stem base, represented here), even though they have differing leaf areas. Instead of variation in mean conduit diameter (A), they should differ only in total conduit number (B), with conduit number scaling isometrically with leaf area across conspecifics of the same height.

seems likely that conductive systems in the root–shoot system in which conduit number remains constant base-to-tip should always be favoured over those with rampant proliferation of conduits base-to-tip (‘furcation’).

#### Revising Leonardo

The notion that conductive systems in plant shoots should be furcated is currently widespread, and we suspect that this widespread acceptance is due to da Vinci’s Rule. The ‘rule’ was introduced innocently enough by Leonardo da Vinci, who noted that to draw a tree that looks nice in a painting, an artist can imagine that the sum of the areas of the terminal twigs is equal to the area at the base (da Vinci and Richter, 1998). This goes for all levels of branching. da Vinci’s ‘rule’ has two components. One is that the sum of the areas of daughter branches is equal to the area of the subtending mother branch, so-called area-preserving branching (Long, 1994; Sone *et al.*, 2009; Minamino and Tateno, 2014). The other aspect of da Vinci’s rule is cylindrical branch segments. This is the notion that, between branching points, branch segments are cylindrical, with the same sapwood area at the tip as at the base of a branch segment. Together, area-preserving branching and cylindrical branches lead to the inevitable conclusion that the summed sapwood area at the tip of a tree is equivalent to the sapwood

area at the base of the tree. Remarkably, neither the expectation of area-preserving branching nor cylindrical branch segments have been extensively tested.

We suspect that da Vinci’s rule is one reason that leads plant biologists to invoke furcation in stems, as they struggle to reconcile what they see under the microscope with da Vinci’s implication of constant sapwood area base-to-tip along a tree. At the shoot base, conduits are wide, and there are comparatively few of them per unit cross-section of secondary xylem. At the shoot tip, conduits are narrow, and there are many of them per unit xylem cross-section (Chen *et al.*, 2012; Olson *et al.*, 2014, 2020; see data in Koçillari *et al.*, 2021). To calculate the total number of conduits at any given point on the stem, it is necessary to multiply the density of conduits per unit cross-sectional area by total sapwood cross-sectional area. Because da Vinci’s rule tells us that total sapwood cross-sectional area is the same at the stem tip as at the base, then high conduit density at the tip necessarily means there must be a vastly higher total number of conduits at the shoot tip than at the base. Furcation is thus introduced to account for this conclusion.

We suggest that instead of pointing toward rampant furcation in the shoot, it seems more plausible that trees do not in fact follow da Vinci’s rule. Tip-to-base conduit widening, together with ultra-widening increases in permeability with height growth, appear sufficient on their own to maintain conductance constant to the leaves, with a constant number of conduits base-to-tip (Echeverría *et al.*, 2019; Koçillari *et al.*, 2021). As a result, there is no need for postulating proliferation of conduits (‘furcation’) in the shoot (Rosell and Olson, 2019). If conduits are constant in number base-to-tip, and conduit density is much higher at the tip than at the base, then this must imply that across species the shoot segments between branching points tend to be narrower apically than basally, or that the sum of daughter branch area is less than mother branch apical area. Certainly the abundant forestry literature that documents taper of tree boles from the trunk base to the base of the crown is consistent with the idea that shoot segments taper rather than remaining of constant diameter à la da Vinci (King and Loucks, 1978; Waring, 1983; Guiterman *et al.*, 2011; Schneider, 2018; McTague and Weiskittel, 2021; Rais *et al.*, 2021). The base-to-tip tapering of branch segments between branching points, and area-preserving branching need broad testing after 500 years of invoking da Vinci’s rule. We are hard-pressed to think of any other postulate that is this consequential that has been left so unexamined for so long.

Stems in which total sapwood area tapers base-to-tip, rather than remaining constant, would, for the same plant height and trunk base sapwood area, be of less volume and therefore cost less in terms of carbon than da Vinci-style shoots with similar amounts of sapwood at the tip as at the base. As a result, given variation between individuals within a population, selection should, all else being equal, favour tapered over da Vinci-type branch architectures. This prediction underscores the importance of selection honing the leaf area–living sapwood area relationship.

*Selection on shoot conduit diameter should affect leaf length, and vice versa*

One way that stem–leaf vascular coordination probably occurs is through variation in leaf size (Lechthaler *et al.*, 2020;

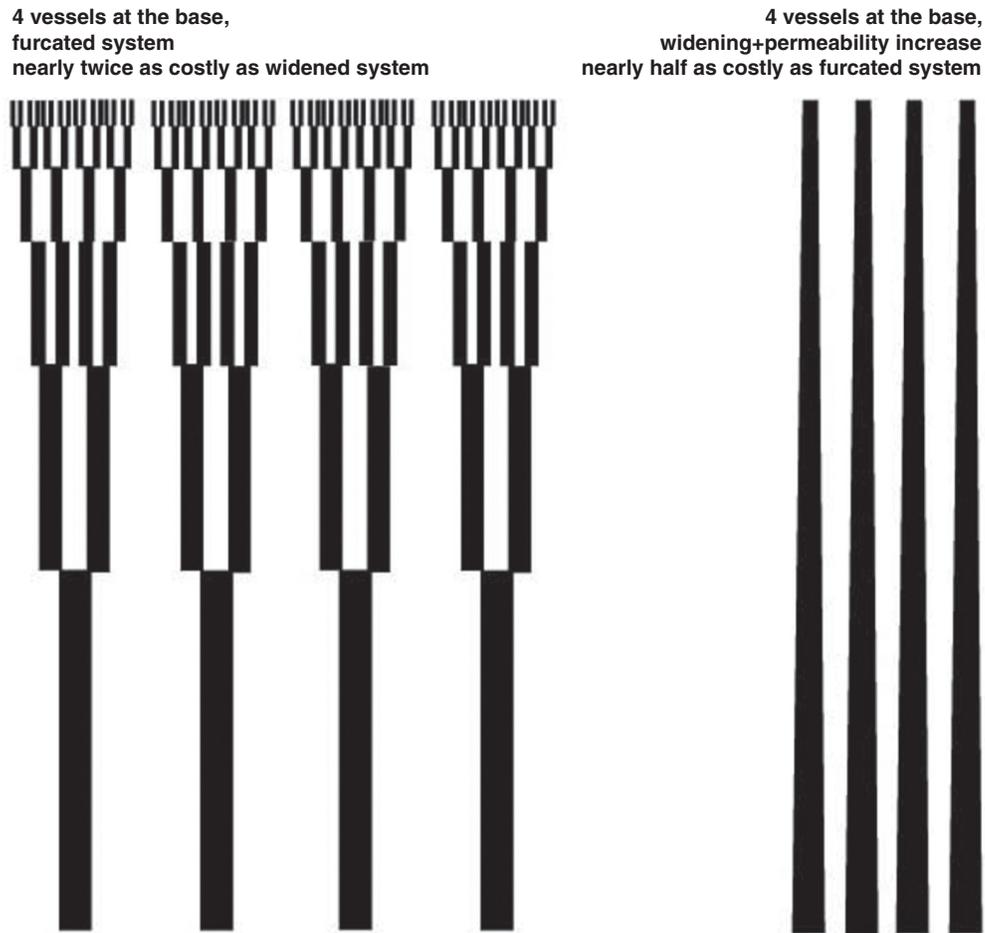


FIG. 7. Furcation, redundancy and carbon cost. For a given number of conduits at the stem base, furcated conductive systems are much more costly than Widened Pipe Model-type systems. Furcated systems are those in which conduits are very numerous at the tip, and coalesce basipetally. We represent here a system with six orders of branching at left. At right is a Widened Pipe Model-type system (Rosell and Olson, 2019; Koçillari *et al.*, 2021) with the same number of conduits basally. Widened Pipe Model-type systems have constant numbers of conduits tip-to-base, and these conduits widen tip-to-base. The widened system costs about half in terms of carbon as compared to the furcated system. The much lower carbon cost of Widened Pipe Model-type systems as compared to furcated ones makes it probable that selection does not favour extensive furcation in the secondary xylem. We represent conduits as widening evenly along their lengths because this makes widening easier to see. However, widening in real conduits follows a power law, with widening being rapid near the stem tip and much slower (more uniform diameters) along most of the length of the conductive path.

Olson *et al.*, 2021). Changes with height growth in conduit diameter and number in the root–shoot system should be most conspicuous in species in which leaf size varies greatly from seedling to large plants. Petiole base conduit diameter scales with leaf length at about twice the rate of that between conduit diameter and stem length (Sack *et al.*, 2012; Lechthaler *et al.*, 2019). This means that small changes in leaf length lead to large changes in petiole base conduit diameter. Petiole base conduit diameter and twig apex conduit diameter are probably closely positively correlated Cao *et al.*, (2022). Petiole base–twig tip conduit diameter correlation would mean that, given a constant rate of tip-to-base conduit widening, a plant with large leaves would have wider conduits at the twig tip and therefore throughout the shoot–root system, as compared to a plant of the same height but with smaller leaves. One way that the marked adjustment in conduit diameter and number per unit leaf area could alter with height growth is an increase in leaf length. An

increase in leaf length would be associated with wider terminal twig conduits, and therefore conduits that are wider, and potentially fewer, along the entire shoot, consistent with empirical observations (Cao *et al.*, 2022), including the tendency for leaf size to scale with plant height in angiosperms (Gleason *et al.*, 2018) and the increase in terminal twig vessel diameter with height across species (Olson *et al.*, 2014, 2021). Longer leaves mean that more of the total pathlength tip-to-base widening occurs in leaves as opposed to stems. This leads to the expectation that conduit diameter should be more constant tip-to-base in stems in large-leaved plants, with widening more marked in smaller-leaved plants (see data in Koçillari *et al.*, 2021). This reasoning leads to the remarkable implication that natural selection favouring a given conduit diameter in the shoot should affect leaf length. By the same token, selection increasing or decreasing leaf length should also alter conduit diameters in the root–shoot system.

*Interplay of hydraulic traits leading to constant leaf hydraulic conductance with height growth*

Given the interplay between leaf and stem traits, it is entirely plausible that trees maintain conductance constant with height growth. Both empirical (Echeverría *et al.*, 2019) and theoretical (West *et al.*, 1999; Savage *et al.*, 2010) studies suggest that selection should favour plants in which leaves maintain the same potential performance values as an individual tree grows taller. The most direct expression of this expectation is that whole tree conductance ( $G_t$ ) should scale isometrically with leaf area ( $A_L$ ) or, in other words, that leaf-specific conductance should remain constant as a tree grows taller.

An essential aspect determining xylem conductivity is variation in the diameters of xylem conduits (Tyree and Ewers, 1991). Because xylem conduit diameter can be easily predicted as a function of the distance from the leaf/stem tip, it is appropriate to express variation in hydraulic traits and  $A_L$  with tree height ( $H$ ). Hence, it is possible to estimate the scaling of  $G_t$  as the product of height raised to three different scaling exponents:

$$G_t \propto H^w \cdot H^p \cdot H^{nt} \quad (1)$$

$H^w$  and  $H^p$  refer to hydraulic properties of a single conduit ( $G_{sc}$ ) running from roots to the leaves (as in the ‘tubes’ of West *et al.*, 1999). In real plant conductive systems, conduits are not continuous tip-to-base (Ewers *et al.*, 1990; Tyree and Ewers, 1991; Comstock and Sperry, 2000; Jacobsen *et al.*, 2012), but previous work shows that selection acts on conduit diameter as though conduits were continuous, meaning that they can be depicted as such for first-order modelling (Koçillari *et al.*, 2021).  $H^{nt}$  refers to the scaling of the numbers of conduits in relation to  $A_L$  or  $H$ .

$H^w$  is the scaling of whole-conduit conductance with height growth as a function of tip-to-base widening only ( $w$ ). Different conduits that differ only in widening rate will have different resistances and thus conductances. The value of the  $H^w$  exponent depends on the degree of conduit diameter ( $D_h$ ) widening with  $H$ , which varies slightly from species to species and between plant organs (in stems, from 0.1 to 0.3 in most cases, generally around 0.2; around 0.5 in angiosperm leaves). It is possible to calculate how the  $G_{sc}$  of a single tube changes with  $H$  (i.e. the  $G_{sc} \propto H^w$  scaling exponent) with simple models varying the degree of widening and tube length. Tip-to-base widening of conduits with height growth means that hydraulic resistance accumulates more slowly as a tree grows taller, and therefore conductive pathlength increases, compared to conduits that remain constant in diameter. This amelioration of resistance due to increasing pathlength is the ‘compensation effect’ with tree height predicted by West *et al.* (1999). The degree of widening is not enough to fully compensate for the growth in height of the trees (i.e. the increase in pathlength) (Fig. 3A) (Olson *et al.*, 2021).

The value of the exponent  $H^p$  represents ultra-widening permeability, the variation in permeability over and above conduit widening with height growth. Ultra-widening permeability is a property not included previously in any model of plant hydraulics. As discussed above, the permeability of a single tube can be increased by increasing the diameter of the conduit apex (Fig. 4). Because conduits widen tip-to-base, a wider apex means a conduit that is wider throughout its length compared

to a conduit of similar length and tip-to-base widening rate but with a narrower apical conduit diameter. An increase in apical conduit diameter with plant height has been demonstrated to occur in angiosperms both at the interspecific level (Zach *et al.*, 2010; Olson *et al.*, 2018, 2021) as well as within a single species (Echeverría *et al.*, 2019). In the latter study, the scaling exponent of the diameter of the apex with tree height was close to 0.25 and therefore the permeability might be roughly estimated as  $(0.25)^4$ , i.e. scaling as  $H^1$ , because a very large part of the resistance is confined near the apex of the tube.

The exponent  $H^{nt}$  represents the scaling of the total number of conduits with  $H$  or with  $A_L$  (because  $A_L$  scales with  $H$ ). It has been proposed that conduit number scales isometrically with  $A_L$  (Shinozaki *et al.*, 1964a; West *et al.*, 1999) or that the number (at the stem base) scales hypo-allometrically (slope <1) due to vessel furcation (or coalescence) (Savage *et al.*, 2010). In either case, the cost of construction and maintenance is predicted to increase greatly with tree size, because  $A_L \propto M_T^{3/4}$ , where  $M_T$  is individual total body mass, and thus the proportion of tissue dedicated to water transport increases proportionally more than  $A_L$  (note that we are not debating whether or not the  $A_L \propto M_T$  exponent is 3/4 or 2/3, etc.; what most current theories have in common is that they posit  $A_L \propto M_T$  exponents of less than one).

In contrast to  $A_L \propto M_T^{3/4}$ , we propose a different view, with our main hypothesis being that natural selection favours variants with isometric scaling between metabolically active sapwood mass and  $A_L$ . This implies that the scaling of conduit number of should be hypo-allometric relative to  $A_L$  but that their total conductance keeps pace with  $A_L$ . This scaling should be observed both at the tree top and at the stem base because furcation within the stem is probably negligible.

The algebraic sum of the exponents  $w$ ,  $p$ , and  $nt$  should be equal to  $\lambda$ , that is the exponent of the scaling relationship of  $A_L$  with tree height, namely  $A_L \propto H^\lambda$ . An example of such an interplay of xylem properties is offered by the data of Echeverría *et al.* (2019) in the tree *Moringa oleifera*. They documented the following allometric relationships empirically:

- scaling of leaf area  $A_L \propto H^{1.86}$ .
- axial conduit widening  $D_h \propto H^{0.07}$ , which implies an exponent  $w = -0.65$ . Axial conduit widening lowers the resistance that otherwise would accumulate with height growth, but it is not sufficient to ameliorate it entirely (Fig. 3). The next exponent represents ultra-widening permeability. The exponent  $w$  is negative because it represents the slight drop in conductance that accumulates with height growth, because widening alone is not sufficient to maintain conductance constant. As a result, selection must favour other mechanisms that provide additional permeability.
- conduit diameter at the stem apex  $D_a \propto H^{0.26}$ , and thus the exponent  $p = 1.04$  (i.e. the flow is proportional to the 4th power of vessel diameter, and the resistance is concentrated mainly at the treetop).  $D_a$  probably increases with  $H$  because taller *Moringa* plants have on average longer leaves (cf. Cao *et al.*, 2022).
- scaling of conduit number  $N_c \propto H^{1.5}$ , so the value of the exponent  $nc = 1.5$ . Because of the scaling between leaf area and height, this implies that  $N_c \propto A_L^{0.8}$ . In other words, the number of conduits per unit leaf area decreases with growth

in height, a result consistent with our prediction that transverse sapwood area per unit leaf area should decrease as an individual grows in height.

Given these empirical exponents and eqn (1), we have:

$$G_t \propto H^{-0.65} * H^{1.04} * H^{1.5}, \text{ then } G_t \propto H^{1.89}$$

This result shows that the exponent of the scaling of whole-tree conductance with height growth is almost identical to the scaling of leaf area with height growth, which was  $A_L \propto H^{1.86}$ . This result is exactly what would be expected if a tree maintains isometry between whole-tree conductance and leaf area as it grows in height ( $G_t \propto A_L^1$ ).

Similar to West *et al.* (1999) and Savage *et al.* (2010), leaf-specific conductivity at the stem base ( $K_0/N_{\text{leaves}}$  in Savage *et al.*, 2010) scales as the 0.25 power of plant mass and, therefore, isometrically with  $H$ . In our example,  $K_0/N_{\text{leaves}}$  scales as the 1.04 power of  $H$ , with our model implying that the same conductance is achieved with a much lower number of xylem conduits because of ultra-widening permeability. This much lower number of xylem conduits implies a lower carbon cost than a system with a higher number of conduits. For the same conductance, selection should favour the variant with the lowest carbon cost. The potential of ultra-widening permeability to contribute to the maintenance of conductance while maintaining carbon cost constant per unit leaf area underscores the importance of testing the hypothesis of ultra-widening permeability empirically.

#### *Trees stop height growth at the conduit diameter permitted by embolism risk*

Conduit diameter is probably shaped to a large degree by its association with vulnerability to embolism. While the exact mechanism connecting vulnerability to drought-induced embolism to conduit diameter remains to be determined (Lens *et al.*, 2022), much evidence suggests that wider conduits are more vulnerable to drought-induced embolism than narrow ones (Anfodillo and Olson, 2021; Rosner *et al.*, 2021; Hacke *et al.*, 2023; Jacobsen and Pratt, 2023; Olson *et al.*, 2023). Likewise, narrower conduits are more resistant to freezing-induced embolism (Davis *et al.*, 1999; Cavender-Bares and Holbrook, 2001; Cavender-Bares, 2005; Ball *et al.*, 2006; Cobb *et al.*, 2007; Sevanto *et al.*, 2012).

The vulnerability–diameter link probably participates in selection on conduit diameter variation within individuals. The tip-to-base profile of conduit widening should reflect a balance between conductive efficiency and ‘safety’, understood as resistance to embolism. Conduits that are maximally wide from their terminal tips all the way to the shoot base would minimize resistance for a given pathlength and basal conduit diameter. However, they would not only cost more in terms of carbon than ones that widen tip-to-base, they would also, assuming a vulnerability–diameter link, expose plants to greater risk of embolism. There is a gradient in pressure in the shoot xylem, with pressures being highly negative at the twig tip and less highly negative toward the shoot base (Lechthaler *et al.*, 2020). If more highly negative pressures are associated with a greater risk of gas embolism, then tip-to-base conduit widening should track vulnerability. Selection shaping the tip-to-base conduit

widening profile should thus be a delicate ‘negotiation’ between opposing vectors of selection. One is selection favouring wider conduits by virtue of their lower hydraulic resistance and the other is selection favouring narrower conduits by virtue of their embolism resistance (Koçillari *et al.*, 2021).

The vulnerability–diameter link also probably participates in variation in plant height across species and even individuals of a species. A pervasive observation is that tree height varies given environmental conditions (Givnish *et al.*, 2014; Larjavaara, 2014). For example, mahogany trees are tallest where moisture availability is higher, and shorter in drier habitats (Chambers-Ostler *et al.*, 2022). Even at the same site, adjacent members of the same species can be of very different heights, for example tall individuals on deep soil and short ones on adjacent rocky outcrops. This variation in height given environmental conditions suggests the existence of a plastic response in plants that sets plant height. It implies that plants have stretch receptors or other mechanisms that detect xylem and/or soil water potentials. It implies that they have adaptive plastic responses that set conduit diameters as a function of the embolism risk posed by these water potentials. Because the main driver of conduit diameter is stem length, via tip-to-base conduit widening, plants achieve a certain conduit diameter, say at the stem base, via a given height. Such a plastic response would explain why plants are shorter on rocky outcrops while adjacent conspecifics on deep soil grow tall. It would also contribute to explaining why trees grow to different maximum heights across habitats that differ in water availability and cold (Givnish *et al.*, 2014; Olson *et al.*, 2018; Fajardo *et al.*, 2020; Chambers-Ostler *et al.*, 2022).

#### *Departure from the ‘packing limit’*

Plants depart from basic expectations of the ‘packing limit’ in ways that are consistent with our hypothesis. The ‘packing limit’ refers to the tradeoff between conduit density (number per unit xylem transectional area) and diameter (Zanne *et al.*, 2010; Chen *et al.*, 2012; Hietz *et al.*, 2017). ‘Packing’ refers to how many conduits can be fit into a given transectional area of xylem (Martinez-Vilalta *et al.*, 2012). There is a ‘limit’ because a given area can be occupied by either one large conduit or many small ones, but not many large ones (Tyree and Ewers, 1991). If xylem conduit density–diameter relations were a simple tradeoff between maximum conduit number for a given xylem area and individual conduit area, then the density–individual conduit area relationship would follow a slope of  $-1$ . However, in large datasets, the slope of the relationship is consistently recovered as  $>-1$  (Fig. 8). This means that, as conduit diameter increases, there are more conduits per unit xylem transectional area than would be expected.

An increase in conduit density for a given diameter is consistent with ‘stretching’. Conduit diameter widens predictably with height within and across species. Therefore, wider conduits tend to be found in taller plants (Olson *et al.*, 2021). Moreover, taller plants have more conduits per unit xylem transectional area than shorter plants (Olson *et al.*, 2020). ‘Stretching’ implies that the transverse area of sapwood corresponding to a given unit of leaf area becomes narrower and narrower as an individual tree grows taller. Natural selection should favour adaptations in the form of adjustments to anatomical structure that

maintain conductance, as well as the costs of xylem construction and maintenance, constant per unit leaf area. In addition to factors of ultra-widening permeability such as wider conduits at the stem tip and more permeable membranes, an increase in conduit density for a given conduit diameter would also lead to an increase in permeability per unit xylem cross-sectional area. Because it could contribute to an increase in permeability, departure from the packing limit is consistent with selection favouring the maintenance of constant leaf-specific conductance given ‘stretching’.

Departure from the packing limit is also consistent with ‘stretching’ given that it could plausibly contribute to maintaining leaf-specific sapwood carbon costs constant with height growth. In angiosperms, an increase in vessel density for a given vessel diameter with height growth (Olson *et al.*, 2014, 2020) can be regarded as deviation of carbon from imperforate tracheary elements and parenchyma to vessels. Similarly, an increase in tracheid density for a given tracheid diameter in conifers (Fig. 8) can be regarded as deviation of carbon from axial parenchyma and rays to tracheids. Shifting investment of carbon from other cell types to conduits as a tree grows taller is one more mechanism by which trees could maintain constant sapwood carbon costs per unit leaf area as they grow taller. ‘Stretching’ posits that selection should favour constant per-leaf area sapwood volumes with height growth. In a small plant, this volume is transectionally wide and therefore can be occupied by abundant non-conduit cell types, and abundant conduits, and still meet the conductive demand of the leaves. In a taller plant, this volume is transectionally narrower but must still meet the conductive demand of the leaves. Deviating some carbon from non-conduit cells to conduits could help keep the carbon cost of the volume corresponding to a given leaf area constant.

#### The need to revise data on sapwood area (as in the Huber value)

Our hypothesis suggests that emphasis on cross-sectional xylem area needs modification. Currently, functional xylem

biologists commonly use indices such as the Huber value (sapwood area divided by leaf area) or leaf-specific conductivity (stem conductivity/leaf area) (Cruziat *et al.*, 2002). If we are correct, then at least two considerations suggest that these indices require overhauling. One consideration is that conduits widen tip-to-base (Koçillari *et al.*, 2021) and sapwood area also increases tip-to-base for the same leaf area (Soriano *et al.*, 2020). As a result, sapwood area, and thus the Huber value and leaf-specific conductivity, vary depending on where the sapwood is sampled even if it subtends the same leaf area (see graphs in Soriano *et al.*, 2020). Sapwood area and conduit diameter are lower closer to the leaves, and become larger moving down the shoot. The predictable increase in sapwood area moving down the trunk is reason enough to require revising the Huber value and similar indices standardizing by plant height (Fig. 9).

Moreover, the possibility of ‘stretching’ and the transverse narrowing of per-leaf area xylem transectional area with height growth is another reason why simply measuring sapwood area or conductivity at a given point is unlikely to reflect the true, whole-pathlength conductance experienced by the leaves. Natural selection is likely to act on the leaf area–metabolically active sapwood volume relationship much more significantly than on the leaf area–sapwood area relationship, wherever that might be measured. ‘Stretching’ predicts that the sapwood area at any point subtending a given amount of leaf area will decrease with height growth, while the permeability will increase. Therefore, measuring sapwood area without taking into account plant height will produce data with significant noise added by sampling from unknown locations along the trajectory of sapwood area narrowing with height. For example, given two plants of the same leaf area, sampling a short plant would lead to the conclusion that it has a very low leaf area/sapwood area ratio, whereas sampling a taller one would give the impression of a high leaf area/sapwood area ratio, when in fact they are on the same leaf area–sapwood volume trajectory (Fig. 10). Given this possibility, it seems important to revisit sapwood area as a functionally relevant metric by examining how it relates to leaf area with changes in plant height.

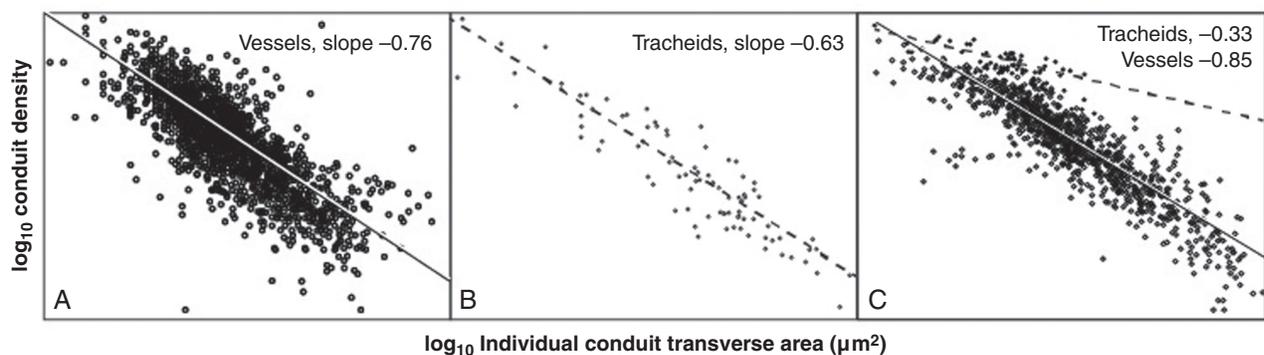


FIG. 8. Departure from the expected slope of the ‘packing limit’. If wood were made up only of conduits, then the relationship between conduit density (conduits  $\text{mm}^{-2}$  of xylem transection) and the mean lumen area of individual conduits would have a slope of  $-1$ . The actual slopes observed are consistently higher (less negative) than this expected value. For example, (A) across angiosperms and gnetophytes in the publications of Sherwin Carlquist (Echeverría *et al.*, 2022), the vessel density–vessel area relationship has a slope of  $-0.76$ ; (B) the relationship between tracheids per square millimetre and tracheid area across 86 conifer species (unpublished data) has a slope of  $-0.63$ ; and (C) in data from Koçillari *et al.* (2021), tracheid-bearing species, including arborescent monocots, conifers, *Ginkgo*, cycads and vesselless ‘dicots’, scale with a slope of  $-0.33$ , while vessel-bearing angiosperms and gnetophytes scale with a slope of  $-0.85$ . Points are species means in A and B, and mean conduit diameters from tip-to-base conduit widening profiles in C. In general, wider conduits are found in taller plants; the much greater density than expected of wider conduits is consistent with natural selection favouring greater permeability per unit xylem transectional area with height growth, associated with sapwood ‘stretching’.

Our hypothesis suggests that, at a minimum, distance from the stem tip needs to be included as a covariable, and comparable points need to be sampled on the stem (Figs 9 and 10). If we are correct, then it is necessary to collect a new set of Huber value data across species with proper standardization. It would then be possible to say that *for the same height*, X species has higher or lower whole-pathlength conductance per unit leaf area than species Y.

#### ‘Shoot’ sapwood, but also roots

Studies of the scaling between leaves and sink tissues tend to focus on scaling of leaf area with shoot sapwood (e.g. Cermák and Nadezhdina, 1998; McDowell *et al.*, 2002; Buckley and Roberts, 2006), for the obvious reasons that shoots are easier to access and because wood is of interest for human use. However, total sink tissues include not just shoots but also roots. Like stems, roots are metabolically active, with fine roots alone representing a very large carbon sink, perhaps 20 % of global net primary productivity (Ruf and Brunner, 2003; McCormack *et al.*, 2015). Leaf area should scale with the total root–shoot sink. The fact that shoot sapwood volume appears to scale isometrically with leaf area (Table 1) suggests that the root sink scales isometrically with the shoot sink. If shoot sapwood volume scaled isometrically with leaf area, but the root sink varied idiosyncratically across species, there would be no consistent pattern of association in shoot volume–leaf area data. Consistent with these expectations, below-ground biomass does appear to scale isometrically with above-ground biomass (Hui *et al.*, 2014). Therefore, the reasoning presented above regarding natural selection favouring isometric scaling between leaf area and sink tissues in the shoot should apply equally well to the entire root–shoot system.

#### Not just sapwood: the bark sink

Sapwood is not the only sink in the root–shoot system, with living bark also representing a major sink. Bark is made up of all of the tissues outside the vascular cambium. Its living, metabolically active tissues include, from inside to out, the active phloem, the non-translocating phloem, and the phelloderm and phellogen. In the many species that lack rhytidome (successive periderms), there is also a secondary cortex that is living (Rosell *et al.*, 2014, 2021; Rosell, 2016, 2019). There is evidence that the metabolic rate of the living bark is much higher than that of the sapwood, meaning that the bark is a significant sink (Rosell *et al.*, 2021, 2023). These same studies also provide reason to suspect that bark metabolic rate scales isometrically with that of the sapwood. For one, bark density and sapwood density scale isometrically across species (Rosell *et al.*, 2014). Density should be associated with metabolic rate, with lower density wood and bark having lower metabolic rates than higher density wood and bark (Lambers *et al.*, 1998; Chapotin *et al.*, 2006; Castorena, 2016; Castorena *et al.*, 2022). Isometric scaling of wood and bark density suggest that wood and bark metabolic rate also scale isometrically. Nitrogen and phosphorus concentrations scale isometrically between living bark and sapwood, in both roots and shoots (Rosell *et al.*, 2023). Nitrogen concentrations are strongly correlated with metabolic rate and lifespan

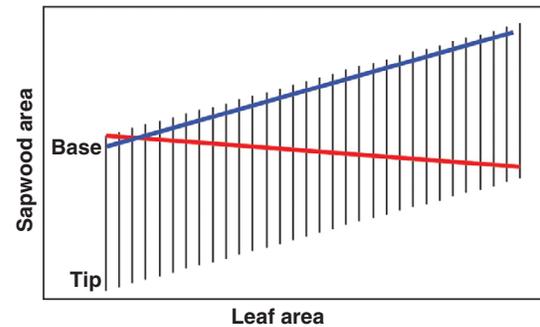


FIG. 9. Rethinking the Huber value. This plot shows sapwood area against leaf area. The vertical lines represent values from single individuals. Each vertical line represents a different individual. ‘Tip’ denotes sapwood area measured directly beneath the foliage. ‘Base’ denotes sapwood area measured at the stem base. Sapwood area increases predictably tip-to-base, so where it is measured on the stem drastically affects the absolute Huber value calculated. Currently available data rarely quantify where along the stem the Huber value was measured. Therefore, current values could lead to spurious conclusions; for example, the red line suggests a negative relationship across individuals. Instead, careful standardization, with measurements from comparable points on different plants, from plants of known heights and known distances from the stem tip, would permit valid conclusions such as ‘species A supports higher leaf area for a given sapwood area as compared to species B’ (blue line).

in leaves (Wright *et al.*, 2004), and there is every reason to think that they should also be with living wood and bark tissue volumes (Castorena *et al.*, 2022). Bark is photosynthetic in twigs and often on main stems, and the contribution of bark photosynthesis to overall carbon economy remains to be understood (Franco-Vizcaíno *et al.*, 1990; Teskey *et al.*, 2008; Rosell *et al.*, 2014, 2021). However, following the reasoning presented above, the net effect of any photosynthetic activity in the bark should lead to source–sink isometry. As suggested by Rosell (2019), living bark volume – in roots and shoots – probably scales isometrically with leaf area. As a result, leaf area should scale isometrically with the total sink, which includes the frequently studied sapwood, but also the living bark in both shoots and roots.

#### The living sapwood is not just parenchyma

Surprisingly little is known about the histological distribution of metabolic activity in the secondary xylem. In conifers, conduction and support are carried out by tracheids, which are dead at maturity, and the living cells in the secondary xylem are axial and ray parenchyma, which make up an interconnected network that ensures that most tracheids are in contact with a living cell at some point (Kedrov, 2012; Carlquist, 2017, 2018; Šlupianek *et al.*, 2021). However, in many, and probably most, angiosperms, the secondary xylem contains living imperforate tracheary elements, either libriform fibres or fibre-tracheids (Olson, 2023; Plavcová *et al.*, 2023). Imperforate tracheary elements and axial parenchyma are derived from the same cambial initials. Therefore, they begin life at the same size and shape. Typically, imperforate tracheary elements elongate intrusively as they mature and do not divide transversely into two or more separate cells. For their part, axial parenchyma cambial derivatives do not elongate, and usually do divide into two or more separate cells, forming a ‘strand’ of axial parenchyma. There

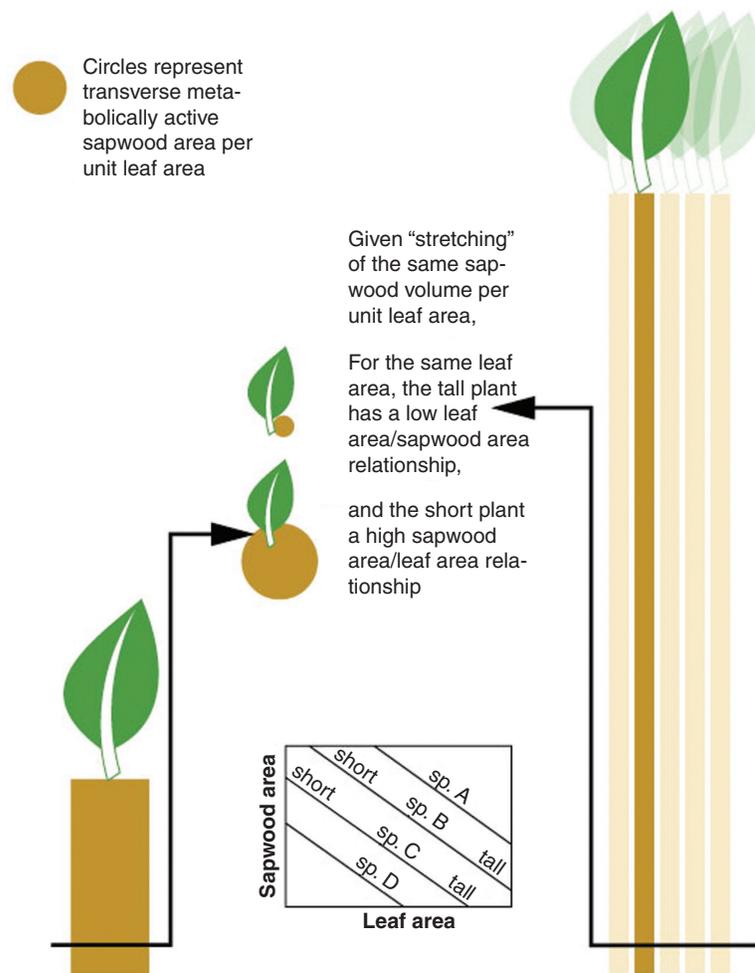


FIG. 10. ‘Stretching’ and the leaf area–sapwood area relationship. Using similar conventions as Fig. 2, we illustrate why variables such as the Huber value and leaf-specific conductivity need to take plant height into account. At middle are the per-leaf area transverse sapwood areas at the base of the trunk of the same individual at different heights, to show that the same leaf area should correspond to increasingly less sapwood area per unit leaf area with height growth. Therefore, the Huber value or leaf-specific conductivity need to be compared across individuals taking plant height into account. At bottom is a representation of the probable landscape of variation in Huber value, which probably scales broadly similarly across species, with variation in y-intercept with variation in variables such as wood density (e.g. Hietz *et al.*, 2017).

is, however, a morphological and functional continuum across species between living imperforate tracheary elements and axial parenchyma. For example, a cambial derivative that neither elongates nor divides into a strand is intermediate between these cell types. In some species, storage of water and starch in the axial system (i.e. not the rays) occurs in living imperforate tracheary elements, not in axial parenchyma (Carlquist, 2015; Olson, 2023; Plavcová *et al.*, 2023). The network of living cells almost certainly closely parallels the network of conductively active conduits. Functional conduits provide water and nutrients to living xylem cells, and the living xylem cells can load sugars into functional conduits in functions such as osmotic regulation of conduction, embolism repair and mobilization of starch in fuelling leaf flushing (Chapotin *et al.*, 2006; Nardini *et al.*, 2011; Brodersen and McElrone, 2013; Konrad *et al.*, 2019). Therefore, metabolically active secondary xylem cells should be adjacent to conductively active conduits (see Jacobsen *et al.*, 2018 on functional lifespans of conduits). How metabolically active cells are distributed in stems, why they occur where

they do, how metabolic rate varies within the living sapwood and how the ‘stretched’ living network interacts with the dead conductive network with its ultra-widening permeability in achieving an isometric balance with the leaves are all virtually unexplored frontiers (the few data available include Chapotin *et al.*, 2006; Spicer and Holbrook, 2007; Castorena, 2016).

## CONCLUSION

Our perspective suggests that increasing sink tissue to leaf area relationships are implausible causes of forest mortality. There is no doubt that total shoot biomass (sapwood + heartwood, living and dead bark) increases relative to leaf area with height growth in trees (Vanninen *et al.*, 1996; Niklas and Enquist, 2001). Above, though, we give reasons to suspect that it is unlikely that sink tissues increase per unit leaf area with height growth. This means that a greater risk of carbon starvation is unlikely to explain the preferential mortality of large individuals.

Instead, there are reasons to expect that embolism vulnerability increases as an individual grows taller. For one, given tip-to-base conduit widening, conduits become predictably wider as an individual grows taller (Koçillari *et al.*, 2021; Olson *et al.*, 2021). Wider conduits are probably more vulnerable to embolism than narrow ones (Sevanto *et al.*, 2012; Hacke *et al.*, 2023; Jacobsen and Pratt, 2023; Olson *et al.*, 2023), though the mechanism connecting vulnerability to diameter remains to be worked out in detail (Lens *et al.*, 2022). Thus, if taller plants have wider conduits, and wider conduits are more vulnerable to embolism, then all else being equal, taller plants should be more vulnerable to embolism, consistent with experimental observations (Olson *et al.*, 2018) and data from wild plants (Bennett *et al.*, 2015; Rowland *et al.*, 2015). In addition to tip-to-base conduit widening, ‘stretching’ of per-leaf area sapwood volumes and consequent reduction of per-leaf area xylem transectional area with height growth should also increase vulnerability to embolism in taller trees. This is because ‘stretching’ means that

selection should favour higher permeability in larger plants. Higher permeability can result from anatomical changes such as vessels that are wider throughout their lengths, inter-vessel pits with thinner inter-vessel pit membranes relative to vessel diameter, or tracheids with larger margo openings. Any of these are likely to be associated with greater vulnerability to embolism (e.g. Li *et al.*, 2016). As a result, our hypothesis not only suggests that sink tissues probably do not increase per unit leaf area with height growth, but also gives reasons to expect that xylem should become more vulnerable to embolism in taller plants.

The plausibility of the causal scenario we outline, and the fact that it is consistent with available empirical data, highlights that major unknowns remain regarding tree structure–function relations, including the sapwood volume–leaf area relationship, da Vinci’s rule, conduit number per unit leaf area and the permeability–height relationship, among others. Given the plausibility of metabolically active sapwood–leaf area isometry, sapwood

TABLE 2. Predictions requiring empirical testing

Prediction	Description
Metabolically active sapwood–leaf area isometry	Selection should favour individuals that maintain living sapwood (plus non-photosynthetic bark tissues and living root)–leaf area relations constant per unit leaf area, because these individuals will have greater carbon surpluses compared to conspecific variants with increasing sink fractions per unit leaf area. Metabolically and conductively active sapwood probably overlap, but this expectation, as well as the relative importance of construction versus metabolic costs as driving selection with respect to leaf area, remain to be determined
‘Stretching’ of per-leaf area sapwood volumes with height growth	If the volume of metabolically active sapwood remains constant per unit leaf area, then as a tree grows taller, per unit leaf area, this constant volume covers a longer vertical distance. The same volume over a longer distance requires it to become narrower transversely (‘stretched’). Sapwood volume should scale with leaf area similarly across species, with variation in the intercept reflecting metabolic rate, ecological strategy, wood density, etc. Practically nothing is known about the absolute volume of sapwood and number of conduits that correspond to a given unit of leaf area across species, but these must be fundamental targets of natural selection shaping plant form and function
Greater permeability of sapwood in taller plants	‘Stretching’ means that there is less sapwood transverse area per unit leaf area in taller plants than short ones. Selection must therefore favour greater permeability in taller plants while maintaining per-leaf area construction and maintenance costs constant, e.g. via fewer, wider vessels or via tracheids with larger pits
Greater permeability in leaves of taller plants	Because so much of the total conductive pathlength resistance is concentrated in leaves, small modifications of leaf structure can potentially lead to marked decreases in resistance, e.g. shorter leaves in conifers toward the tree top, or lower bundle sheath resistance
Greater vulnerability to embolism in taller plants	Tip-to-base conduit widening leads to taller plants having wider conduits. If wider conduits are more vulnerable to embolism, then taller plants should be more vulnerable to embolism. Moreover, the anatomical features that should lead to ultra-widening permeability in taller plants, e.g. pit membrane thickness scaling $<1$ with individual conduit area (Li <i>et al.</i> , 2023), should all also be associated with greater vulnerability to embolism
Constant number of conduits per unit leaf area base-to-tip along stems (no furcation)	Tip-to-base conduit widening, together with ultra-widening permeability, should be sufficient to maintain conductance constant to the leaves as a plant grows taller. This means that, per unit leaf area, there should be a constant number of conduits per unit leaf area along the lengths of stems between conspecifics of the same height. For the same number of conduits basally, a conductive system with a constant number of conduits will cost much less in terms of carbon than a furcated one (with proliferation of conduits apically), and so should be favoured by selection. Very little is known about variation in the number of conduits per unit leaf area across species and ecological strategies
Trees cones, not cylinders: departure from Da Vinci’s rule	Furcation is proposed as a patch to square the observation of high conduit densities at the stem tip with the da Vinci rule notion that the area of sapwood is the same at the tip as at the base. Given that extensive furcation in the stem is unlikely, it is more likely that total sapwood cross-sectional area decreases base-to-tip
Leaf size is involved in changes in conduit number and diameter with height growth	Conduit diameter widens tip-to-base very rapidly in leaves in angiosperms, meaning that slightly larger leaves have much wider conduits at the petiole base. If petiole base and stem tip conduit diameters are correlated, then this means that a plant with large leaves should have wider conduits at the stem tip than an identically sized plant with smaller leaves. Given the same rate of tip-to-base conduit widening, the larger leaved plant will have wider conduits throughout. If conifer leaves have lower widening rates than angiosperm leaves, then changes in leaf length should be especially important in shaping the tip-to-base resistance profiles in conifers
Trees cease height growth at the conduit diameter given embolism risk	If wider conduits are more vulnerable to embolism, and conduits widen predictably with height growth, then plants should cease growth at the height corresponding to the conduit diameter permitted by habitat embolism risk. This implies that plants can detect water potential or some correlate, and have evolved an adaptive plastic response that involves adjustment of conduit diameter via height according to embolism risk

‘stretching’ and many potential sources of ultra-widening permeability, if these do *not* occur, and conductance, photosynthesis and carbon surpluses per unit leaf area really do decrease with height growth, understanding why selection would ‘permit’ sapwood volume to increase per unit leaf area, and conductance to drop per unit leaf area (Buckley and Roberts, 2006) would represent a significant conundrum for empirical research. As a result, testing the predictions we outline in Table 2 promises to help inform mechanistic scenarios regarding woody plant evolution and forest mortality in the face of climate change.

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