

## Viewpoint

# An appreciation of apex-to-base variation in xylem traits will lead to more precise understanding of xylem phenotypic plasticity

### Summary

Xylem air embolism is the primary cause of drought-related tree mortality. Phenotypic plasticity of xylem traits is key for species acclimation to environmental variability and evolution. It is widely believed that plants increase xylem embolism resistance in response to drought. However, I argue that this hypothesis, based on extensive literature, relies on sampling methods that overlook predictable anatomical patterns, potentially biasing our understanding of acclimation and adaptation strategies.

### Hydraulic limitations to photosynthesis

Plant metabolism relies on energy from leaf photosynthesis, which requires tissue hydration to maintain open stomata for CO<sub>2</sub> assimilation. This process results in significant water loss through transpiration, necessitating replenishment to sustain photosynthesis. The xylem sap flow rate must balance leaf transpiration ( $F = ET$ ), which depends on root-to-leaf xylem conductance ( $K_{xyl}$ ) and leaf water potential (according to Darcy law,  $F = K_{xyl} \times \Delta\Psi$ , with  $\Delta\Psi$  being the xylem water potential difference between leaves and the root/soil interface).

Water evaporation from nanopores in leaf mesophyll cells initiates sap ascent through the xylem, driven by a gradient of decreasing tension from twigs to roots. This flow is maintained in liquid form through water molecule cohesion and adhesion to xylem walls (Dixon & Joly, 1895). From a physical perspective, two key principles apply:

(1) As pressure decreases (tension increases), and temperature rises, gas bubbles in xylem sap expand (ideal gas law); and  
(2) Maintaining a liquid phase becomes unsustainable beyond a critical bubble diameter ( $D_{MAX}$ ):  $D_{MAX} = -4\gamma/T$ , where  $\gamma$  is the liquid–gas surface tension (Young–Laplace equation: Pickard, 1981).

As xylem sap flows upwards along a gradient of progressively higher tension, dissolved gas bubbles tend to expand, while  $D_{MAX}$  decreases, thus necessitating mechanisms to avert tension-induced xylem embolism. Water moves between conduits through pit

membranes with nanometric pores that block large nanobubbles, preventing xylem embolization (Zhang *et al.*, 2024). The pectic nature of these membranes allows their permeability to be influenced by the ionic content of the sap (Nardini *et al.*, 2011). Additionally, amphiphilic lipids in the sap can coat nanobubbles, increasing their gas–liquid surface tension, and thus  $D_{MAX}$  (Yang *et al.*, 2020).

Higher tension towards branch apices increases embolism risk but may be mitigated by varying pit traits and sap composition to maintain hydraulic safety margins (i.e. the difference between the minimum xylem water potential ( $\Psi_{xyl}$ ) and  $\Psi_{xyl}$  at which embolism events significantly limit water transport (e.g.  $P50$ , the  $\Psi_{xyl}$  at which 50% of xylem conductivity is lost)) along the xylem hydraulic path. Furthermore, variation in pit traits leading to higher pit permeability from the crown periphery downwards (Schulte, 2012; Lazzarin *et al.*, 2016; Zambonini *et al.*, 2024), that is along a decreasing tension, could enhance xylem conductance ( $K_{xyl}$ ), supporting the balance between transpiration and sap flow ( $ET = F$ ), thus sustaining photosynthesis. However, data on these trait variations is limited.

### Xylem anatomical and hydraulic traits along the hydraulic path

Recent studies show that the axial variation in the mean diameter ( $D$ ) of xylem conduits (including conifer tracheids and angiosperm vessels) in the current annual ring is largely explained by the distance from the apex ( $DFA$ ) ( $R^2 > 0.8$ ). This relationship often follows a power function ( $D = aDFA^b$ ) with the exponent  $b$  ranging from 0.1 to 0.4, varying by species (Anfodillo *et al.*, 2006; Petit *et al.*, 2008, 2010, 2023; Lintunen & Kalliokoski, 2010; Jyske & Hölttä, 2015; Kiorapostolou & Petit, 2019; Lechthaler *et al.*, 2019; Soriano *et al.*, 2020; Koçillari *et al.*, 2021). This  $DFA$ -dependent widening persists during tree development (Petit *et al.*, 2023; Rita *et al.*, 2024), meaning that larger conduits form farther from the apex as the hydraulic path lengthens, regardless of tree age (Petit *et al.*, 2008).

Other anatomical traits also scale with  $DFA$ . Both in angiosperms and in conifers, conduit length increases from apex to base (Sperry *et al.*, 2006). In conifers, various pit traits scale similarly to conduit diameter (Lazzarin *et al.*, 2016; Zambonini *et al.*, 2024). These observations align with analyses showing a constant contribution of lumen resistance to total xylem resistance.

A  $DFA$ -dependent pattern of conduit diameter implies important consequences for xylem hydraulic efficiency and safety: (1) Terminal stem and branch segments act as hydraulic bottlenecks. Larger conduits farther from the apex contribute little to whole-tree hydraulic resistance, ensuring efficient water supply to leaves regardless of tree height (Anfodillo *et al.*, 2013; Lechthaler *et al.*, 2020; Petit *et al.*, 2023);

- (2) The axial gradient in xylem water potential is most pronounced towards the distal end of stems and branches. Decreased pit permeability towards the apex filters against unsustainable gas bubble formation, with xylem resistance to embolism decreasing from apex to base (Zambonini *et al.*, 2024); and
- (3) These findings are consistent with empirical measurements revealing a constant contribution of lumen resistance to total xylem resistance and consistent scaling of various pit traits with *DFA* (Lazzarin *et al.*, 2016; Zambonini *et al.*, 2024).

### A challenge to the concept of adaptive phenotypic plasticity in xylem traits: the importance of sampling design

The growing evidence that xylem anatomical traits vary predictably with the distance from the stem or branch apex (*DFA*) presents a significant challenge for sampling methodology in xylem research. The axial location of samples can greatly influence the observed trait dimensions due to *DFA*-related variations potentially biasing the interpretation of results. For instance, with a scaling exponent  $b$  describing the variation in conduit diameter with *DFA* in the range of 0.2–0.3, the mean conduit diameter will be *c.* 30–40% larger at 10 compared to 30 cm from the apex.

A common practice is to perform anatomical and hydraulic measurements on stem and branch segments of a given age or at the stem or branch base. This method has led to reports that trees from arid environments produce narrow, embolism-resistant conduits, while those in mesic environments produce wider, more conductive conduits. However, plants in dry environments often exhibit slower growth and smaller sizes compared to those in humid conditions.

Fig. 1 illustrates how sampling at a fixed branch age can lead to biased interpretations. This example refers to branch sampling of same tree species characterized by different growth rates. A 3-yr-old branch represents a structure resulting from three successive pulses of growth, with coordinated increases in branch length and diameter. At each growth pulse, the branch apex extends outward from the crown due to primary growth, forming a new xylem layer. The conduits are narrowest just below the branch apex and widen with increased *DFA*. Both fast-growing (Fig. 1a) and slow-growing (Fig. 1b) branches exhibit the same conduit diameter *c.* *DFA* scaling relationship, but their overall anatomical structures differ due to varying elongation rates. (Fig. 1c). At the level of the third internode, which occurs at different distances from the apex, the fast-growing branch has larger conduits than the slow-growing one (Fig. 1d).

To avoid potential bias from single sampling on the branch axis at given internode (i.e. fixed age) in trees with varying growth rates, or from sampling at the base of branches and stems in trees of different overall sizes, it is highly recommended to take multiple samples along the main branch or stem axis (Olson *et al.*, 2020; Zambonini *et al.*, 2024). Crucially, at least a few of those samples should be taken within a short distance from the apex (e.g. 2–3 samples for *DFA* < 15–20 cm) to ensure a more accurate representation of anatomical and hydraulic trait variation. However, only a few studies have examined the effect of growing

conditions on xylem conduit size by assessing the conduit diameter *c.* *DFA* relationship (Petit *et al.*, 2016, 2022; Kiorapostolou *et al.*, 2020). These results showed that limiting conditions such as drought (Petit *et al.*, 2016, 2022) or reduced tree vigor (Kiorapostolou *et al.*, 2020) may stimulate the production of larger conduit diameter. They also reported annual branch elongation rates, allowing for the extrapolation of conduit diameter at a fixed branch age, which resulted in narrower conduits in trees with reduced annual branch elongation (Table 1), simply due to sampling closer to the branch apex (cf. Fig. 1).

The hypothesis of adaptive phenotypic plasticity suggests plants in drier conditions produce narrower, more embolism-resistant conduits. Given that these studies likely compared plants with different growth rates, the perceived adaptive plasticity might actually be sampling bias. By contrast, studies recognizing *DFA*-dependent patterns have reported minimal phenotypic changes or slightly larger conduits in growth-limited plants (Petit *et al.*, 2016, 2022; Olson *et al.*, 2018; Kiorapostolou & Petit, 2019; Fajardo *et al.*, 2020; Kiorapostolou *et al.*, 2020).

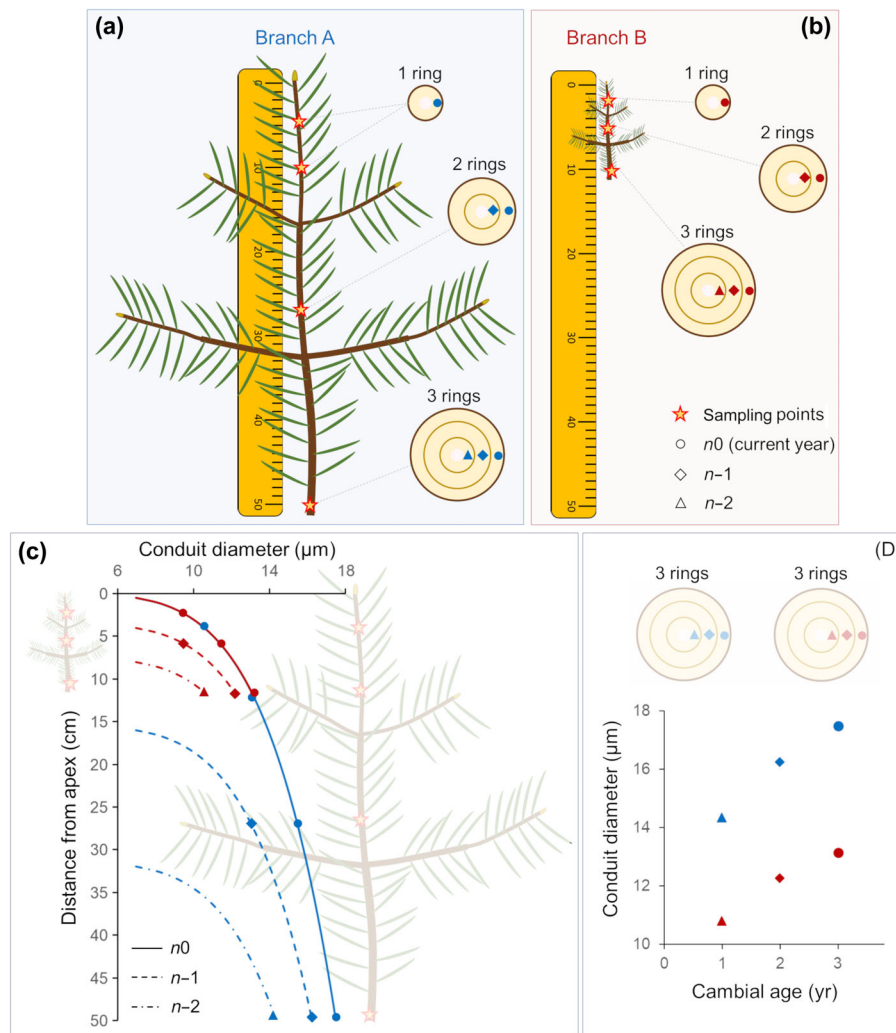
Different sampling approaches leading to opposite results highlight the need to consider the sustainability of contrasting plant responses to drought. Plastic adjustments, such as reduced conduit diameter and pit permeability, increase xylem resistance to embolism but reduce total plant conductance unless significantly more xylem conduits are produced. Conversely, larger conduits may increase or maintain conductance with fewer conduits but increase embolism vulnerability.

Maintaining xylem conductance is crucial for balancing sap flow and leaf transpiration, fundamental for plant survival. These considerations cast doubt on long-held assumptions about plant reactions to environmental variability and emphasize the need for revised methodologies in xylem trait research.

### *DFA*-dependent anatomical patterns and xylem hydraulic properties

Empirical evidence supports that xylem conduit diameter scales with *DFA* to a power of *c.* 0.2. However, data on axial variability in pit traits are limited, mainly focusing on conifers (Schulte, 2012; Lazzarin *et al.*, 2016; Zambonini *et al.*, 2024). This highlights the need for a comprehensive examination of how *DFA* influences anatomical and anatomy-dependent hydraulic traits, such as resistance to tension-induced embolism (e.g. P50) and total xylem conductance ( $K_{xyl}$ ).

Pit traits and conduit lumen diameter impact  $K_{xyl}$  and embolism resistance differently. Pit characteristics, such as size and structure, affect hydraulic safety by preventing the spread of air phases and contribute to hydraulic resistance. Conduit diameter influences efficiency, as lumen conductance scales with the fourth power of its diameter (Hagen–Poiseuille's law: Tyree & Ewers, 1991), but does not guard against embolism. Embolism resistance is typically estimated by measuring the percentage loss of conductance (*PLC*) in xylem samples at different xylem water potentials ( $\Psi_{xyl}$ ). This indicates that while lumen diameter does not cause embolism, it reflects the extent of conductance loss when embolism occurs.



**Fig. 1** The age-related sampling artefact in the assessment of anatomical and anatomy-related functional properties of branches differing in growth rates. (a) Branch structure of a 3-yr-old branch with fast elongation rates (branch A:  $c. 16 \text{ cm yr}^{-1}$ ); (b) branch structure of a 3-yr-old branch with slow elongation rates (branch B:  $c. 4 \text{ cm yr}^{-1}$ ). Sampling points (stars) are identified at increasing distance from the apex on both branch A and branch B at the level of each of the three internodes. Wood samples from current year ( $n0$ ), previous year ( $n-1$ ) and previous-previous year ( $n-2$ ) internode have one, two and three annual rings, respectively, with the outermost being that produced in the current year ( $n0$ ). (c) The individual variability in the diameter of xylem vascular conduits ( $d$ ,  $\mu\text{m}$ ) is shown as the diameter within each ring of each wooden samples extracted in the different internode plotted against the distance from the stem apex ( $DFA$ , cm) (branch A: blue symbols; branch B: red symbols). This result is obtained by assuming that for every year of growth the newly formed conduits down along the whole branch axis (i.e. along the current year, outermost ring) have a diameter dependent on their distance from the branch apex according to the commonly reported axial widening equation  $d = a \times DFA^b$ , where the allometric constant  $a$  and the scaling exponent  $b$  do not vary between branch A and branch B (in this example  $a = 8 \mu\text{m cm}^{-1}$ , and  $b = 0.2$ ). Notably, the conduit diameter in the current year, outermost ring varies axially with  $DFA$  identically in both branch A and branch B. Instead, conduit diameter in inner rings are progressively narrower simply due to the effect of branch elongation in the previous years. (d) Difference in conduit diameter of the different annual rings for branch A and branch B at the level of third internode (3 yr). Conduit diameter increases with cambial age simply because the distance between the apex and the branch segment increases with age due to the annual branch elongation, and branch A has larger conduits simply because the branch elongation rate is higher than branch B.

Pit traits scale with conduit diameter both at the individual (Zambonini *et al.*, 2024) and intraspecific level (Hacke & Jansen, 2009), thus explaining the correlations between conduit diameter and  $P50$ , and between  $P50$  and the xylem-specific hydraulic conductivity ( $k_s$ ) (known as the safety-efficiency trade-off). However, these relationships typically are less clear in interspecific comparisons, especially in meta-analyses aggregating data collected from many studies (Gleason *et al.*, 2016; Hacke *et al.*, 2023).

A recent investigation on two conifer species found that embolism vulnerability in the outermost two to three xylem layers (i.e. rings) progressively increases (i.e.  $P50$  becoming less negative) from the stem apex downwards. The axial scaling of  $P50$  with  $DFA$  showed a power scaling exponent very similar to that of anatomical traits (lumen diameter and pit membrane area) with  $DFA$  (Zambonini *et al.*, 2024). These anatomical data were consistent with existing literature, but the strong power scaling of  $P50$  with

**Table 1** Intraspecific differences in the mean hydraulic diameter of xylem conduits ( $Dh$ : vessels for angiosperms, tracheids for conifers) between populations characterized by different branch or stem annual elongation rates.

Reference	Species	Groups	(A) Axial sampling Widening equation	(B) Common sampling approach		
				Branch age	$DFA$ @ fixed age	$Dh$ @ fixed age
Petit <i>et al.</i> (2016)	<i>Fraxinus ornus</i>	Fast-growing	$Dh = 11.22 \times DFA^{0.41}$	2	56.04	58.46 (+)
		Slow-growing	$Dh = 12.88 \times DFA^{0.44}$ (+)	2	12.20	38.72
Kiorapostolou <i>et al.</i> (2020)	<i>Pinus sylvestris</i>	Healthy	$Dh = 7.19 \times DFA^{0.21}$	3	18.39	13.25 (+)
		Declining	$Dh = 7.59 \times DFA^{0.25}$ (+)	3	7.44	12.53
Petit <i>et al.</i> (2022)	<i>Fagus sylvatica</i>	Control	$Dh = 12.02 \times DFA^{0.20}$	3	87.36	29.39 (+)
		Drought	$Dh = 12.30 \times DFA^{0.20}$ (ns)	3	56.78	27.59

The data are evaluated using two approaches: (A) the relationship between  $Dh$  and the distance from the branch or stem apex ( $DFA$ ); (B) the common approach of estimating  $Dh$  on branch or stem segments of fixed age ( $Dh$  @ fixed age). The distance from the apex of these segments ( $DFA$  @ fixed age) and  $Dh$  @ fixed age are estimated based on the annual elongation rate and the widening equation from the reference study. Data are presented for: (1) Branches of neighboring *Fraxinus ornus* (L.) trees with different branch elongation rates (Petit *et al.*, 2016) (maximum age of sampled branches from fast-growing trees was 2 yr); (2) Terminal stem portions of healthy and vigor-declining mature *Pinus sylvestris* (L.) trees (Kiorapostolou *et al.*, 2020); (3) Branches from the apical part of the crown of *Fagus sylvatica* (L.) trees from a long-term throughfall precipitation exclusion experiment (control vs drought treatments) (Petit *et al.*, 2022). For each sampling approach (A and B), the group with the largest  $Dh$  is indicated with (+). ns indicates no significant difference between groups.

$DFA$  along the stem was unprecedented, covering a significant span of  $P50$  variation ( $> 3$  MPa), that includes most of the interspecific  $P50$  variation reported for conifers (Gleason *et al.*, 2016).

Future studies must evaluate the potential effect of  $DFA$  on hydraulic traits. The common practice of sampling branch segments of fixed age or diameter for hydraulic measurements might introduce bias due to uncontrolled  $DFA$  position during sampling. This issue is particularly relevant for individuals and species with varying growth rates, as illustrated for conduit diameter (Fig. 1).

### Loss of conductivity vs loss of conductance: wood samples vs whole plants

Recognizing  $DFA$ -dependent anatomical and hydraulic traits is crucial for evaluating how tension-induced embolism affects overall conductance ( $K_{xyl}$ ) in living plants or branch segments.

$K_{xyl}$  depends primarily on the small conduits near the stem apex, which have the least conductivity. Larger conduits farther from the apex have higher conductivity, mitigating the impact of increased path length on total xylem conductance (Petit & Anfodillo, 2009). Consequently, the loss of functionality in the small conduits near the stem apex has a profound impact on overall xylem conductance. By contrast, the loss of large conduits near the stem base of tall trees would have limited impact on the total plant conductance ( $K_{xyl}$ ) (i.e. they can be bypassed by the flowing sap). This theoretical consideration aligns with empirical observations showing that extensive sapwood sectioning at the stem base has limited effects on leaf water supply (Dietrich *et al.*, 2018).

$DFA$ -dependent patterns should be considered when evaluating xylem conductance loss in branch samples, especially using methods inducing embolism at specific locations (e.g. air-injection, centrifugation). The apical segment end, with the narrowest and least conductive conduits, represents a hydraulic bottleneck. By contrast, conduits at embolism induction sites are larger and more conductive, implying that more conduits need to

embolize to produce a given conductance loss in longer samples. This implies that the number of embolized conduits required to produce a given loss in conductance of the entire sample theoretically increases with the sample length (i.e. long samples would result to be more embolism resistant than short ones). Notably, the closer the apical sample end is to the actual branch apex, the greater the number of conduits that need to be embolized to trigger a given percent loss of the total sample conductance. These considerations are consistent with observations that  $P50$  estimates using centrifuge techniques, which create a peak of tension in the center of the branch sample, result in more negative values than assessments using the bench dehydration technique, where tension is evenly distributed along the branch axis (Cai *et al.*, 2010). However, a study found no effect of rotor length on  $P50$  estimates using the flow-centrifuge technique (Pivovarov *et al.*, 2016), though crucial details like the distance from the apex of the apical segment cut end were not reported.

This overview emphasizes the need for hydraulic research to account for  $DFA$ -dependent anatomical and hydraulic traits and understand the impact of xylem permeability loss on total plant conductance, depending on embolized conduits' location along the hydraulic path.

### Conclusions

Consistent axial patterns of anatomical and hydraulic traits have been extensively neglected in xylem research, potentially leading to biased empirical support for ecological theories. Xylem phenotypic plasticity is considered crucial for plant acclimation to changing environmental conditions and plays a fundamental role in species evolution. However, the idea that embolism resistance is a key driver for species acclimation and adaptation to dry and warm climates should be reconsidered, considering possible sampling bias and its unsustainability for the plant's carbon economy.

Developing standardized sampling techniques that account for trait correlations with distance from the apex is essential

for building a more robust understanding of how environmental patterns of xylem phenotypic plasticity will shape future forest ecosystems.

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## Competing interests

None declared.

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