

Testing the benefits of early vessel evolution

Adam B. Roddy^{1*}

¹ School of Forestry & Environmental Studies, Yale University, New Haven, CT, USA

* Correspondence: adam.rodny@yale.edu

From rainforests to deserts, across latitudes and elevations, the flowering plants (the angiosperms) dominate almost every terrestrial ecosystem. It is impossible not to be amazed and impressed by their abundance and diversity. While their sudden appearance and rapid domination of the fossil record was once considered a mystery (Friedman, 2009), the keys to their success have increasingly become apparent, although it is all too common to posit that innovations in single aspects of their form and function—e.g. pollination (O’Meara *et al.*, 2016), metabolism (Bond, 1989), genome architecture (Dodsworth *et al.*, 2016), or combinations of them (Simonin and Roddy, 2018)—are solely responsible for angiosperm diversity and dominance.

Many of these key innovations are often posited as originating at the base of the angiosperm clade, yet the heightened diversification rates apparent among angiosperms likely did not occur until after many of these supposed key innovations of the angiosperms had evolved (Sanderson and Donoghue, 1994). In this issue of the *Journal of Experimental Botany*, Trueba *et al.* 2019 show that the putative earliest steps in the evolution of one of these innovations—xylem vessels—does not necessarily deliver the physiological benefits traditionally thought without the evolution of additional anatomical traits in the xylem. Studying the unique flora of New Caledonia—an enviable task indeed!—Trueba *et al.* show that the wood of vesselless angiosperms is no less hydraulically efficient nor more prone to embolism spread than that of closely-related vessel-bearing species with scalariform perforation plates (Fig. 1).

Tradeoffs in hydraulic structure-function among vascular plants

Although there have been many hypotheses proposed to explain the sudden and rapid success of the angiosperms, their heightened metabolic rates have been critical in allowing them to more rapidly grow and outcompete other major lineages (Bond, 1989). Because allowing CO₂ to diffuse into the leaf requires exposing the wet, internal surfaces of the leaf to the dry atmosphere, increasing rates of CO₂ assimilation requires that higher fluxes of water be supplied to the leaf. Transporting higher fluxes of water to support higher rates of photosynthesis is enabled by smaller, more densely packed veins and stomata

that enable unprecedented rates of leaf gas exchange (Franks and Beerling, 2009; Brodribb and Feild, 2010; Boer *et al.*, 2012; Simonin and Roddy, 2018).

However, smaller cells are not always advantageous. While smaller cells enable higher rates of diffusion across cell surfaces, smaller diameter xylem conduits have higher resistance to water flow according to the Hagen-Poiseuille law. In the introduction to their classic paper on size variation in secondary xylem, Bailey and Tupper (1918) focus almost exclusively on the large variation in cell size apparent among plants and animals and then systematically characterize the sizes of secondary xylem elements among vascular plants. They showed that the vessel elements in angiosperms are unique in being short and wide, compared to the narrow tracheids of gymnosperms and cryptogams. Increases in xylem conduit diameter come with substantial physiological gains of increasing the efficiency of water delivery. Although they—and much research since then—has focused on the sizes (i.e. diameter) of xylem elements as a key innovation, the major change is actually one of cell shape.

Furthermore, the plant vascular system is more complex than a set of simple pipes (Lehnebach *et al.*, 2018), and other anatomical features can overwhelm the effects of conduit diameter on xylem hydraulic resistance (Pittermann *et al.*, 2005; Hacke *et al.*, 2007), as Trueba *et al.* show. Tracheids and vessels differ not only in the sizes and shapes of their constituent cells but also in the structure of their intertracheary pits and perforation plates. Indeed, innovations in perforation plates and pit anatomy have been posited as critical to compensating for the increased resistance of smaller diameter cells: the lower hydraulic resistance of torus-margo pits in gymnosperms compensates for the small diameters of their tracheids (Pittermann *et al.*, 2005), and the lower resistance of simple perforation plates between xylem vessel elements in angiosperms (Christman and Sperry, 2010) compensates for the reductions in vein and conduit diameters needed to achieve high leaf vein densities (Feild and Brodribb, 2013). That vesselless and vessel-bearing angiosperms can differ in conduit diameter and still maintain the same hydraulic conductivity points to the role of these other, less apparent anatomical traits in determining hydraulic efficiency (Trueba *et al.* 2019). Overall, the results of Trueba *et al.* reiterate how important the three-dimensional complexity of wood structure is for hydraulic function (Broderson *et al.*, 2019).

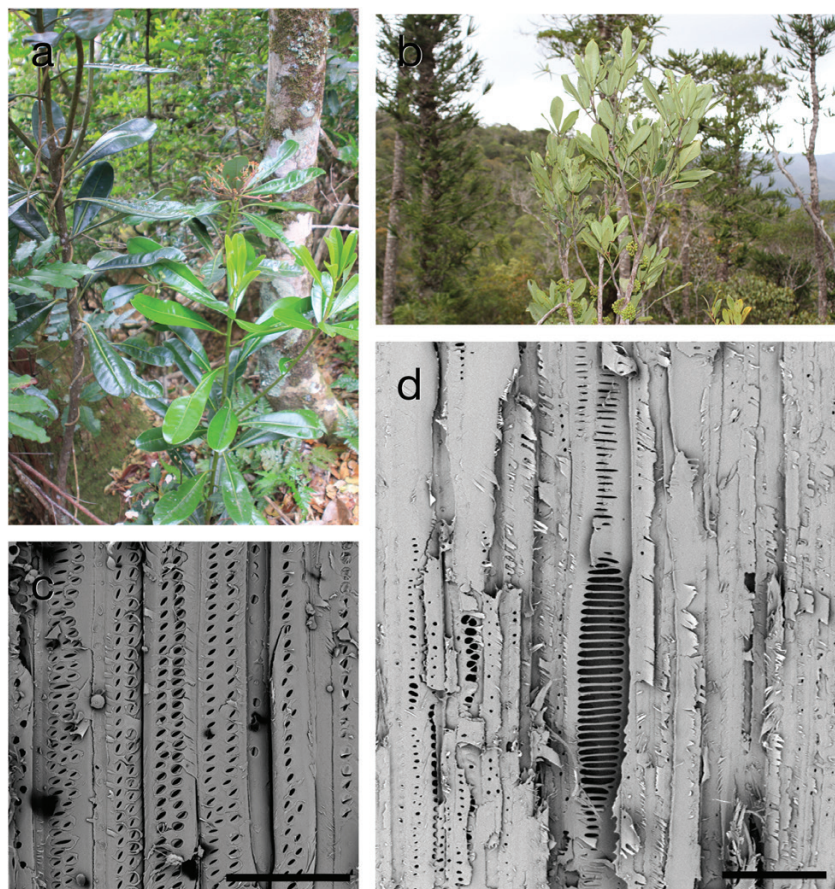


Fig. 1. Images of vesselless and vessel-bearing plants. (a) The vesselless *Zygogynum pancheri* (Winteraceae) growing in New Caledonia. (b) The vessel-bearing *Hedycarya* sp. (Monimiaceae) growing in New Caledonia. (c) Scanning electron microscopy (SEM) image of intertracheary pitting in the vesselless *Zygogynum crassifolium*. (d) SEM image of a scalariform perforation plate in the vessel-bearing *Hedycarya parvifolia*. Scale bars in (c) and (d) are 100 μm . All images courtesy of S. Trueba.

Evolutionary ‘progress’ and the order of trait evolution

Although it is both tempting and appealing to consider the evolution of vessels from tracheid-bearing lineages as indicative of evolutionary progress, such thinking is flawed (Olson, 2012). The major trends of xylem evolution first outlined by Bailey and Tupper (1918) presume that vessels are ‘better’ than tracheids—so much better, in fact, that their evolution is irreversible (Cheadle, 1956). The results of Trueba et al. will hopefully help to overturn such ideas, similar to the work of Pitterman et al. (2005). Such studies show that vessels are not inherently better than tracheids and that the putative earliest steps in vessel evolution may not have brought substantial physiological benefits to vessel-bearing lineages. Only in combination with other anatomical traits, such as modifications to perforation plates and intertracheary pits, may vessels have enabled higher fluxes of water transport. Furthermore, not being able to transport high fluxes of water may not be a significant cost in habitats characterized by low vapor pressure deficits, where early angiosperms may have first appeared (Feild et al., 2003,

2004; Jansen et al., 2004). While it is easy to view the extant ‘basal’ lineages studied by Trueba et al. as relicts of the past, they are still thriving despite having a relatively narrow environmental niche—likely no different from numerous other tropical species.

The traditional view of xylem evolution implicitly assumes that more conductive vessels are more favored by selection. However, anatomical and physiological innovations that, for example, elevate the maximum rate of water flux do not necessarily mean that this combination of traits is the only one that can survive. Rather, the evolution of these new traits and trait combinations expand the range of possible phenotypic solutions without leading to extinction of trait combinations that generate sub-maximal rates of physiological processes—faster is not always better (Bond, 1989). For example, the evolution of smaller cells among the angiosperms lifted the maximum possible rate of photosynthetic metabolism, but this did not mean that the only species that survive are those that operate at this maximum rate of photosynthesis (Simonin and Roddy, 2018).

Nonetheless, how and in what order multiple traits evolve remains an intriguing line of inquiry, one on which

the results of Trueba et al. have some bearing. The higher hydraulic efficiency for which the angiosperms are—rightly or wrongly—known, relies on multiple traits (large diameter conduits, alternate pitting, simple perforation plates, etc.). Given the results of Trueba et al. that there are no differences in hydraulic conductivity or vulnerability to embolism of vesselless and vessel-bearing species with scalariform perforation plates, was there an initial advantage of vessels with scalariform perforation plates? Are modifications to cell shape that enable transitions between tracheids and vessel elements more labile than modifications to pit and perforation plate structure? While it is unclear from the results of Trueba et al. whether tracheary cell shape evolves before or in unison with changes in intertracheary pitting and perforation plate morphology, they have generated new data for rare lineages critical to macroevolutionary studies of correlated trait evolution. Studies like that of Trueba et al., which leverages understudied species to make novel comparisons, are critical to advancing our understanding of the evolution of plant form and function.

A remaining challenge: do differences in conductivity matter?

While the results of Trueba et al., like many other studies, focus exclusively on wood, characterizing how the wood structure–function relationships influence leaf- and canopy-scale processes will be an important advancement. The discrete components that comprise the hydraulic pathway from the soil to the leaf must function in unison to maintain water transport. As plants grow, they build new xylem in the stem and add new leaves, and older stem xylem—like the leaves they once supported—transport less water to the canopy (Melcher *et al.*, 2003). Yet, the most common hydraulic measurements made on stems, including those done by Trueba et al., ignore two key facts: (1) older xylem are likely less functional than newer xylem and (2) conduits are narrower closer to the leaves (Anfodillo *et al.*, 2013), meaning that the apex is the point of highest hydraulic resistance. It is easy to assume that measurements of hydraulic conductivity on excised stems can predict fluxes of water to the leaf (Pivovarov *et al.*, 2014), but depending on how hydraulic resistance is partitioned in the plant, there can be substantial loss of stem hydraulic conductivity with little impact on total shoot hydraulic conductance (Meinzer, 2002). While there is support for positive scaling between stem conductivity and leaf physiological capacity—even from the New Caledonian flora (Brodrribb and Feild, 2000)—a better determination of hydraulic efficiency may be based on water supply all the way to the transpiring leaves (Brodersen *et al.*, 2019). Thus, many reported scaling relationships between shoot and leaf hydraulic capacity may be spurious, unless they explicitly incorporate the entire hydraulic path length (Drake *et al.*, 2015).

References

- Anfodillo T, Petit G, Crivellaro A. 2013. Axial conduit widening in woody species: a still neglected anatomical pattern. *IAWA Journal* **34**, 352–364.
- Bailey IW, Tupper WW. 1918. Size variation in tracheary cells: I. a comparison between the secondary xylems of vascular cryptogams, gymnosperms and angiosperms. *Proceedings of the American Academy of Arts and Sciences* **54**, 149–204.
- de Boer HJ, Eppinga MB, Wassen MJ, Dekker SC. 2012. A critical transition in leaf evolution facilitated the cretaceous angiosperm revolution. *Nature Communications* **3**, 1221.
- Bond WJ. 1989. The tortoise and the hare: Ecology of angiosperm dominance and gymnosperm persistence. *Biological Journal of the Linnean Society* **36**, 227–249.
- Brodersen CR, Roddy AB, Wason JW, McElrone AJ. 2019. Functional status of xylem through time. *Annual Review of Plant Biology* **70**, 407–433.
- Brodrribb TJ, Feild TS. 2000. Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from new caledonian and tasmanian rainforests. *Plant, Cell & Environment* **23**, 1381–1388.
- Brodrribb TJ, Feild TS. 2010. Leaf hydraulic evolution led a surge in leaf photosynthetic capacity during early angiosperm diversification. *Ecology Letters* **13**, 175–183.
- Cheadle VI. 1956. Research on xylem and phloem—progress in fifty years. *American Journal of Botany* **43**, 719–731.
- Christman MA, Sperry JS. 2010. Single-vessel flow measurements indicate scalariform perforation plates confer higher flow resistance than previously estimated. *Plant, Cell & Environment* **33**, 431–443.
- Dodsworth S, Chase M, Leitch AR. 2016. Is post-polyploidization diploidization the key to the evolutionary success of the angiosperms? *Botanical Journal of the Linnean Society* **180**, 1–5.
- Drake PL, Price CA, Poot P, Veneklaas EJ. 2015. Isometric partitioning of hydraulic conductance between leaves and stems: balancing safety and efficiency in different growth forms and habitats. *Plant, Cell & Environment* **38**, 1628–1636.
- Feild TS, Brodrribb TJ. 2013. Hydraulic tuning of vein cell microstructure in the evolution of angiosperm venation networks. *New Phytologist* **199**, 720–726.
- Feild TS, Arens NC, Dawson TE. 2003. The ancestral ecology of angiosperms: emerging perspectives from extant basal lineages. *International Journal of Plant Sciences* **164**, S129–S142.
- Feild TS, Arens NC, Doyle JA, Dawson TE, Donoghue MJ. 2004. Dark and disturbed: a new image of early angiosperm ecology. *Paleobiology* **30**, 82–107.
- Franks PJ, Beerling DJ. 2009. Maximum leaf conductance driven by CO₂ effects on stomatal size and density over geologic time. *Proceedings of the National Academy of Sciences, USA* **106**, 10343–10347.
- Friedman WE. 2009. The meaning of Darwin's 'abominable mystery'. *American Journal of Botany* **96**, 5–21.
- Hacke UG, Sperry JS, Field TS, Sano Y, Sikkema EH, Pittermann J. 2007. Water transport in vesselless angiosperms: conducting efficiency and cavitation safety. *International Journal of Plant Sciences* **168**, 1113–1126.
- Jansen S, Bass P, Gasson P, Lens F, Smets E. 2004. Variation in xylem structure from tropics to tundra: evidence from vested pits. *Proceedings of the National Academy of Sciences, USA* **101**, 8833–8837.
- Lehnebach R, Beyer R, Letort V, Heuret P. 2018. The pipe model theory half a century on: a review. *Annals of Botany* **121**, 773–795.
- Meinzer FC. 2002. Co-ordination of vapour and liquid phase water transport properties in plants. *Plant, Cell & Environment* **25**, 265–274.
- Melcher PJ, Zwieniecki MA, Holbrook NM. 2003. Vulnerability of xylem vessels to cavitation in sugar maple. Scaling from individual vessels to whole branches. *Plant Physiology* **131**, 1775–1780.
- Olson ME. 2012. Linear trends in botanical systematics and the major trends of xylem evolution. *The Botanical Review* **78**, 154–183.
- O'Meara B, Smith S, Armbruster WS, *et al.* 2016. Non-equilibrium dynamics and floral trait interactions shape extant angiosperm diversity. *Proceedings of the Royal Society B: Biological Sciences* **283**, 20152304.

- Pittermann J, Sperry JS, Hacke UG, Wheeler JK, Sikkema EH.** 2005. Torus-margo pits help conifers compete with angiosperms. *Science* **310**, 1924.
- Pivovarov AL, Sack L, Santiago LS.** 2014. Coordination of stem and leaf hydraulic conductance in southern California shrubs: a test of the hydraulic segmentation hypothesis. *New Phytologist* **203**, 842–850.
- Sanderson MJ, Donoghue MJ.** 1994. Shifts in diversification rate with the origin of angiosperms. *Science* **264**, 1590–1593.
- Simonin KA, Roddy AB.** 2018. Genome downsizing, physiological novelty, and the global dominance of flowering plants. *PLoS Biology* **16**, e2003706.
- Trueba S, Delzon S, Isnard S, Lens F.** 2019. Similar hydraulic efficiency and safety across vesselless angiosperms and vessel-bearing species with scalariform perforation plates. *Journal of Experimental Botany* **70**, 3227–3240.