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COMMENTARY

The recurrent evolution of extremely resistant xylem

Scott A. M. McAdam[1] · Amanda A. Cardoso[1]

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Abstract

- ***Key message*** **Highly resistant xylem has evolved multiple times over the past 400 million years.**
- ***Context*** Water is transported under tension in xylem and consequently is vulnerable to invasion by air and the formation of embolism. A debate has raged over whether embolism formation is non-reversible occurring at low water potentials or a regular diurnal occurrence that is non-lethal because of a capacity to refill embolised conduits.
- ***Aims*** This commentary is on a recent article, which utilised new non-invasive imaging techniques for assessing the formation of embolism in xylem, finding that the xylem of *Laurus nobilis* was highly resistant to the formation of embolism.
- ***Methods*** The recent results of this discovery are placed in the context knowledge from a diversity of species that has so far been identified with xylem similarly highly resistant to embolism formation.
- ***Results*** The discovery that *L. nobilis* has xylem highly resistant to embolism formation adds to a body of literature suggesting that the resistance of xylem to embolism formation is a key adaptation utilised by many species native to seasonally dry environments. Highly resistant xylem has evolved numerous times across the angiosperm clade.
- ***Conclusion*** With more studies utilising similar observational and direct methods of assessing embolism resistance, further insight into the ecological and evolutionary relevance of this trait is imminent.

Keywords Xylem · Vulnerability · Evolution · Embolism · Drought

The high diffusivity of carbon dioxide in air compared to liquid water provided a strong selective pressure for land plants to evolve more than 400 million years ago (Raven 2002). While it is comparatively easy to obtain carbon dioxide from the atmosphere, terrestrial photosynthesis comes at the cost of transpiration (Wong et al. 1979). To maintain the hydration of internal tissues, plants have evolved a suite of traits including a water impermeable cuticle, stomata to regulate gas exchange, and an internal water transport system of xylem elements to supply aerial tissue with water from the soil. All of these anatomical adaptations are essential for determining the rate of water loss from a plant, yet the vulnerability of the xylem to invasion by air under negative tension (i.e. embolism) alone determines the lethal water potential threshold for land plants (Brodersen et al. 2011; Brodribb et al. 2016, 2017; Choat et al. 2012, 2016; Cochard et al. 2015).

In a recent study, Lamarque et al. (2018) elegantly illustrate the importance of xylem resistance in determining a lethal water potential threshold in the Mediterranean tree *Laurus nobilis* L. This observation, as their title suggests, is somewhat inconvenient for a conventional wisdom that suggests xylem cavitation-induced embolism is a regular, non-lethal occurrence. This idea stems from indirect and destructive methods such as bench dehydration, air injection and centrifugation (Torres-Ruiz et al. 2017) for determining the percentage of embolised vessels in the xylem. The conclusion from most of these studies, many based on observations in *L. nobilis*, has been that a high percentage of vessels experience daily cycles of embolism and refilling (Hacke and Sperry 2003, Salleo et al. 2004, Trifilò et al. 2014). As a result, these studies could mistakenly lead one to conclude that xylem vulnerability to embolism plays little or no role in determining the threshold water potential at which plants die under water stress.

There has been much debate in recent years about the validity of these indirect and destructive methods,

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✉ Scott A. M. McAdam
smcadam@purdue.edu

[1] Department of Botany and Plant Pathology, Purdue Center for Plant Biology, Purdue University, 915 W. State St, West Lafayette, IN 47907, USA

particularly those that involve observations in species with long vessels (Choat et al. 2010; Cochard et al. 2010; Hacke et al. 2015; Jacobsen and Pratt 2012; Torres-Ruiz et al. 2017). With knowledge of the methodological limitations and the long vessels of *L. nobilis*, Lamarque et al. (2018) employed two non-invasive methods, i.e. MicroCT and the optical method (Brodribb et al. 2016, 2017), in leaves and stems to construct vulnerability curves, as well as centrifugation in branch segments that exceeded the length of the longest vessel. Contrary to 25 years of results using methods prone to artefacts, this species was found to have xylem that is extremely resistant to the formation of embolism, with the water potential at which 50% of the xylem is embolised (P_{50}) being − 7.9 MPa in stems and − 8.3 MPa in leaves. These results are unsurprising given that during drought, *L. nobilis* can survive with little or no leaf damage until − 9.0 MPa (Lamarque et al. 2018). Furthermore, during summer, field-grown plants still have open stomata at a water potential of − 2.4 MPa (Salleo et al. 2009), a negative water potential previously believed to cause around 90% embolised vessels (Hacke and Sperry 2003).

A remarkable result emerging from the work of Lamarque et al. (2018), and other recent studies using direct methods to quantify xylem vulnerability (Brodribb et al. 2017; Rodriguez-Dominguez et al. 2018; Skelton et al. 2017; Torres-Ruiz et al. 2017), is that highly resistant xylem is commonly observed in species native to dry or arid environments. This observation supports the idea that resistant xylem is adaptively relevant for plant survival during periods of water deficit and for the radiation of species into dry environments. In the conifers, for instance, P_{50} is a well-known trait associated with species evolution into dry environments (Brodribb et al. 2014; Larter et al. 2017). Many species of derived Cupressaceae and Taxaceae live in very dry environments and have xylem that is highly resistant to embolism (Brodribb et al. 2014; Larter et al. 2017). It is in this group of conifers that the species with the most resistant xylem so far recorded, *Callitris tuberculata*, native to arid areas of southwest Australia, evolved, with a P_{50} of − 18.8 MPa (Larter et al. 2015).

A literature review reveals that, currently, at least 136 species, from both gymnosperm and angiosperm lineages, have evolved highly resistant xylem (i.e. arbitrarily defined here as a P_{50} less than − 5.0 MPa) (Fig. 1). From this brief analysis of the literature, there seems to be very little phylogenetic signal in the occurrence of highly resistant xylem, with species being found across the seed plant phylogeny in 62 genera and 20 orders. The large number of convergent evolutionary transitions towards highly resistant xylem so far reported in angiosperms is reminiscent of the number of evolutionary transitions into aquatic habitats (Cook 1999) or deciduousness in this lineage (Axelrod 1966). Ancestral state reconstruction in the conifers

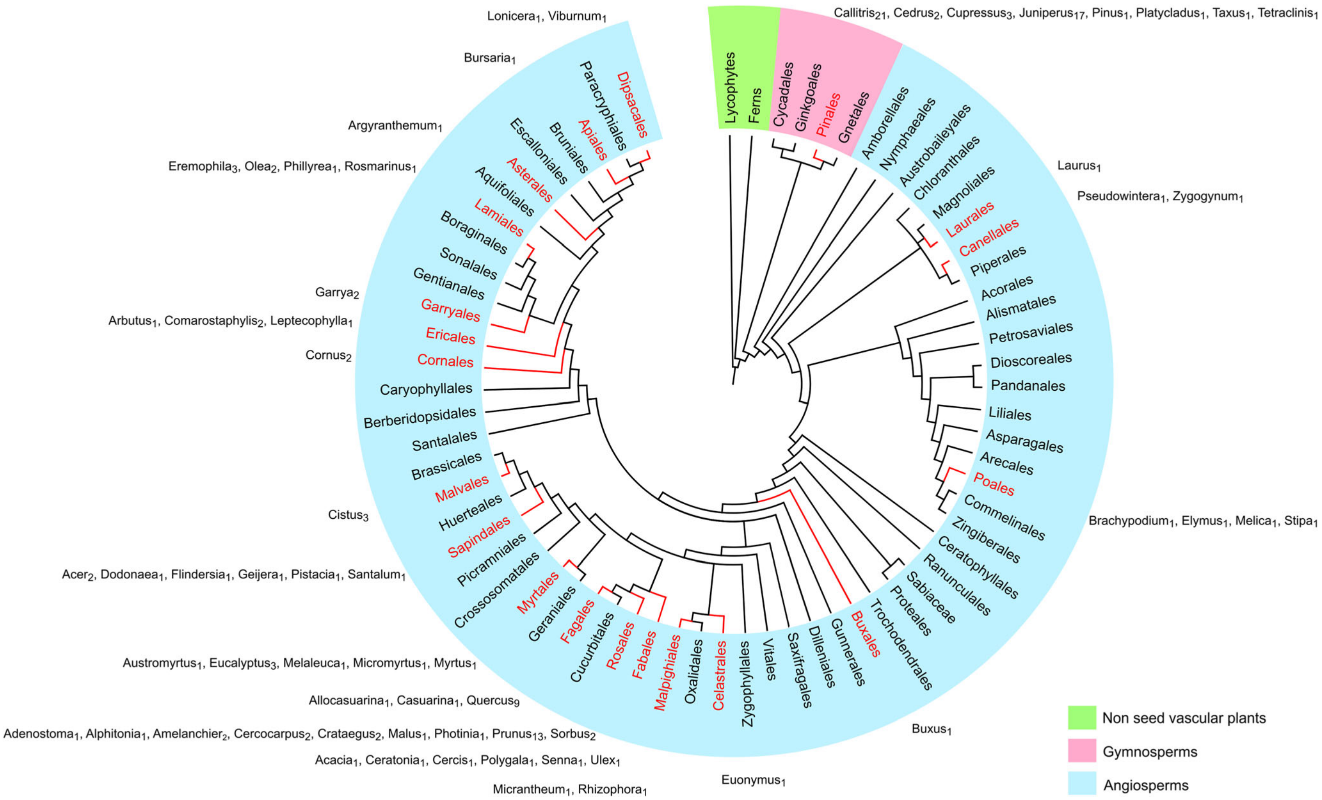

Fig. 1 Phylogenetic distribution of orders (displayed in red) and associated genera containing plant species with highly resistant xylem (defined at a $P_{50} < -5$ MPa). Numbers following each genus indicate the number of species so far identified in each genus (see Supporting Table S1 for the dataset used in this phylogenetic analysis)

suggests that the last common ancestor of this lineage had xylem that was vulnerable to embolism formation (Brodribb et al. 2014; Pittermann et al. 2012). While the xylem physiology of early diverging angiosperms is understudied, many of these lineages are either native to ever-wet, understorey tropical environments or are aquatic, it is likely that the xylem of the common ancestor of all angiosperms was likewise highly vulnerable (Feild and Holbrook 2000; Hacke et al. 2007).

The recent results of Lamarque et al. (2018) add the first species, to this ever-growing list, from the early diverging order Laurales. The family Lauraceae is believed to have had an origin in ever-wet temperate and tropical forests, with an abundance of genera today dominating tropical cloud forests (Chanderbali et al. 2001; Donoghue 2008). It is believed that *L. nobilis* is a relict of a Tethyan rainforest flora that dominated the Mediterranean basin until the Pliocene (Rodríguez-Sánchez et al. 2009). The evolution of highly resistant xylem in this species may be related to the survival of this lineage in the Mediterranean basin during the acidification over the past 30 million years. Unlike the Lauraceae, which is so far only represented by a single species with highly resistant xylem, some genera contain many species with highly resistant xylem (Fig. 1). One such genus is *Quercus* with nine species so far identified with highly resistant xylem (Bhaskar et al. 2007; Dietrich et al. 2018; Lobo et al. 2018; Martin-StPaul et al. 2014; Scoffoni et al. 2017; Skelton et al. 2018; Vaz et al. 2012; Vilagrosa et al. 2003). Many of the angiosperms species so far identified are native to particularly dry regions of the globe, such as central and southern Australia, the Mediterranean basin and southwest North America. The broad phylogenetic spread of species so far identified with highly resistant xylem suggests a strong selective pressure on the evolution of this trait (Choat et al. 2012, 2018).

We do not yet know what specific anatomical or physiological traits are responsible for the evolution of highly resistant xylem, although a number have been proposed. These include xylem cell wall thickness (Blackman et al. 2010; Cardoso et al. 2018), pit membrane thickness (Choat et al. 2006; Hacke et al. 2006; Jansen et al. 2009; Pittermann et al. 2010; Wheeler et al. 2005) and the consistency of surfactants in the xylem (Schenk et al. 2015). It could be that each evolutionary transition towards highly resistant xylem was the result of modification to a different trait or set of traits, influencing xylem physiology. In *L. nobilis*, Lamarque et al. (2018) and Klepsch et al. (2018) suggest pit membrane thickness is the primary driver behind the evolution of highly resistant xylem. Comparative anatomy and physiology focusing on small clades in which highly resistant xylem has a single, recent evolutionary origin could provide a powerful tool to further investigate the key anatomical or physiological traits controlling xylem resistance to embolism formation. Using this approach, we may finally be able to answer questions about the molecular regulation of this critical trait. While many future studies are possible from the use of direct methods for observing embolism formation in the xylem, the simple phylogenetic analysis presented here suggests that further studies in species native to dry environments should ensure that highly resistant xylem becomes a truth universally acknowledged.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Axelrod DI (1966) Origin of deciduous and evergreen habits in temperate forests. Evolution 20:1–15

Bhaskar R, Valiente-Banuet A, Ackerly DD (2007) Evolution of hydraulic traits in closely related species pairs from mediterranean and nonmediterranean environments of North America. New Phytol 176:718–726

Blackman CJ, Brodribb TJ, Jordan GJ (2010) Leaf hydraulic vulnerability is related to conduit dimensions and drought resistance across a diverse range of woody angiosperms. New Phytol 188:1113–1123

Brodersen CR, Lee EF, Choat B, Jansen S, Phillips RJ, Shackel KA, McElrone AJ, Matthews MA (2011) Automated analysis of three-dimensional xylem networks using high-resolution computed tomography. New Phytol 191:1168–1179

Brodribb TJ, McAdam SAM, Jordan GJ, Martins SC (2014) Conifer species adapt to low-rainfall climates by following one of two divergent pathways. Proc Natl Acad Sci U S A 111:14489–14493

Brodribb TJ, Bienaimé D, Marmottant P (2016) Revealing catastrophic failure of leaf networks under stress. Proc Natl Acad Sci U S A 113:4865–4869

Brodribb TJ, Carriqui M, Delzon S, Lucani C (2017) Optical measurement of stem xylem vulnerability. Plant Physiol 174:2054–2061

Cardoso AA, Brodribb TJ, Lucani CJ, DaMatta FM, McAdam SAM (2018) Coordinated plasticity maintains hydraulic safety in sunflower leaves. Plant Cell Environ 41:2567–2576

Chanderbali AS, Werff H, Renner SS (2001) Phylogeny and historical biogeography of Lauraceae: evidence from the chloroplast and nuclear genomes. Ann Mo Bot Gard 88:104–134

Choat B, Brodie TW, Cobb AR, Zwieniecki MA, Holbrook NM (2006) Direct measurements of intervessel pit membrane hydraulic resistance in two angiosperm tree species. Am J Bot 93:993–1000

Choat B, Drayton WM, Brodersen C, Matthews MA, Shackel KA, Wada H, McElrone AJ (2010) Measurement of vulnerability to water stress-induced cavitation in grapevine: a comparison of four techniques applied to long-vesseled species. Plant Cell Environ 33:1502–1512

Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Field TS, Gleason SM, Hacke UG, Jacobsen AL, Lens F, Maherali H, Martínez-Vilalta J, Mayr S, Mencuccini M, Mitchell

PJ, Nardini A, Pittermann J, Pratt RB, Sperry JS, Westoby M, Wright IJ, Zanne AE (2012) Global convergence in the vulnerability of forests to drought. Nature 491:752–755

Choat B, Badel E, Burlett R, Delzon S, Cochard H, Jansen S (2016) Noninvasive measurement of vulnerability to drought-induced embolism by X-ray microtomography. Plant Physiol 170:273–282

Choat B, Brodribb TJ, Brodersen CR, Duursma RA, López R, Medlyn BE (2018) Triggers of tree mortality under drought. Nature 558: 531–539

Cochard H, Herbette S, Barigah T, Badel E, Ennajeh M, Vilagrosa A (2010) Does sample length influence the shape of xylem embolism vulnerability curves? A test with the Cavitron spinning technique. Plant Cell Environ 33:1543–1552

Cochard H, Delzon S, Badel E (2015) X-ray microtomography (micro-CT): a reference technology for high-resolution quantification of xylem embolism in trees. Plant Cell Environ 38:201–206

Cook CD (1999) The number and kinds of embryo-bearing plants which have become aquatic: a survey. Perspect Plant Ecol Syst 2:79–102

Dietrich L, Delzon S, Hoch G, Kahmen A (2018) No role for xylem embolism or carbohydrate shortage in temperate trees during the severe 2015 drought. J Ecol:1–16

Donoghue MJ (2008) A phylogenetic perspective on the distribution of plant diversity. Proc Natl Acad Sci U S A 105:11549–11555

Feild TS, Holbrook NM (2000) Xylem sap flow and stem hydraulics of the vesselless angiosperm Drimys granadensis (Winteraceae) in a Costa Rican elfin forest. Plant Cell Environ 23:1067–1077

Hacke UG, Sperry JS (2003) Limits to xylem refilling under negative pressure in Laurus nobilis and Acer negundo. Plant Cell Environ 26:303–311

Hacke UG, Sperry JS, Wheeler JK, Castro L (2006) Scaling of angiosperm xylem structure with safety and efficiency. Tree Physiol 26: 619–701

Hacke UG, Sperry JS, Feild TS, Sano Y, Sikkema EH, Pittermann J (2007) Water transport in vesselless angiosperms: conducting efficiency and cavitation safety. Int J Plant Sci 168:1113–1126

Hacke UG, Venturas MD, MacKinnon ED, Jacobsen AL, Sperry JS, Pratt RB (2015) The standard centrifuge method accurately measures vulnerability curves of long-vesselled olive stems. New Phytol 205:116–127

Jacobsen AL, Pratt RB (2012) No evidence for an open vessel effect in centrifuge-based vulnerability curves of a long-vesselled liana (Vitis vinifera). New Phytol 194:982–990

Jansen S, Choat B, Pletsers A (2009) Morphological variation of intervessel pit membranes and implications to xylem function in angiosperms. Am J Bot 96:409–419

Klepsch M, Zhang Y, Kotowska MM, Lamarque LJ, Nolf M, Schuldt B, Torres-Ruiz JM, Qin DW, Choat B, Delzon S, Scoffoni C, Cao KF, Jansen S (2018) Is xylem of angiosperm leaves less resistant to embolism than branches? Insights from microCT, hydraulics, and anatomy. J Exp Bot:1–13

Lamarque LJ, Corso D, Torres-Ruiz JM, Badel E, Brodribb TJ, Burlett R, Charrier G, Choat B, Cochard H, Gambetta GA, Jansen S, King A, Lenoir N, Martin-StPaul N, Steppe K, Bulcke JV, Zhang Y, Delzon S (2018) An inconvenient truth about xylem resistance to embolism in the model species for refilling Laurus nobilis L. Ann For Sci 75: 88

Larter M, Brodribb TJ, Pfautsch S, Burlett R, Cochard H, Delzon S (2015) Extreme aridity pushes trees to their physical limits. Plant Physiol 168:804–807

Larter M, Pfautsch S, Domec JC, Trueba S, Nagalingum N, Delzon S (2017) Aridity drove the evolution of extreme embolism resistance and the radiation of conifer genus Callitris. New Phytol 215:97–112

Lobo A, Torres-Ruiz JM, Burlett R, Lemaire C, Parise C, Francioni C, Truffaut L, Tomášková I, Hansen JK, Kjær ED, Kremer A, Delzon S (2018) Assessing inter-and intraspecific variability of xylem vulnerability to embolism in oaks. For Ecol Manag 424:53–61

Martin-StPaul NK, Longepierre D, Huc R, Delzon S, Burlett R, Joffre R, Rambal S, Cochard H (2014) How reliable are methods to assess xylem vulnerability to cavitation? The issue of ‘open vessel’ artifact in oaks. Tree Physiol 34:894–905

Pittermann J, Choat B, Jansen S, Stuart SA, Lynn L, Dawson TE (2010) The relationships between xylem safety and hydraulic efficiency in the Cupressaceae: the evolution of pit membrane form and function. Plant Physiol 153:1919–1931

Pittermann J, Stuart SA, Dawson TE, Moreau A (2012) Cenozoic climate change shaped the evolutionary ecophysiology of the Cupressaceae conifers. Proc Natl Acad Sci U S A 109:9647–9652

Raven JA (2002) Selection pressures on stomatal evolution. New Phytol 153:371–386

Rodriguez-Dominguez CM, Carins Murphy MR, Lucani C, Brodribb TJ (2018) Mapping xylem failure in disparate organs of whole plants reveals extreme resistance in olive roots. New Phytol 218:1025–1035

Rodríguez-Sánchez F, Guzmán B, Valido A, Vargas P, Arroyo J (2009) Late Neogene history of the laurel tree (Laurus L., Lauraceae) based on phylogeographical analyses of Mediterranean and Macaronesian populations. J Biogeogr 36:1270–1281

Salleo S, Lo Gullo MA, Trifilo P, Nardini A (2004) New evidence for a role of vessel-associated cells and phloem in the rapid xylem refilling of cavitated stems of Laurus nobilis L. Plant Cell Environ 27:1065–1076

Salleo S, Trifilò P, Esposito S, Nardini A, Gullo MAL (2009) Starch-to-sugar conversion in wood parenchyma of field-growing Laurus nobilis plants: a component of the signal pathway for embolism repair? Funct Plant Biol 36:815–825

Schenk HJ, Steppe K, Jansen S (2015) Nanobubbles: a new paradigm for air-seeding in xylem. Trends Plant Sci 20:199–205

Scoffoni C, Albuquerque C, Brodersen C, Townes SV, John GP, Bartlett MK, Buckley TN, McElrone AJ, Sack L (2017) Outside-xylem vulnerability, not xylem embolism, controls leaf hydraulic decline during dehydration. Plant Physiol 173:1197–1210

Skelton RP, Brodribb TJ, McAdam SAM, Mitchell PJ (2017) Gas exchange recovery following natural drought is rapid unless limited by loss of leaf hydraulic conductance: evidence from an evergreen woodland. New Phytol 215:1399–1412

Skelton RP, Dawson TE, Thompson SE, Shen Y, Weitz AP, Ackerly D (2018) Low vulnerability to xylem embolism in leaves and stems of North American oaks. Plant Physiol 177:1066–1077

Torres-Ruiz JM, Cochard H, Choat B, Jansen S, López R, Tomášková I, Padilla-Díaz CM, Badel E, Burlett R, King A, Lenoir N, Martin-StPaul NK, Delzon S (2017) Xylem resistance to embolism: presenting a simple diagnostic test for the open vessel artefact. New Phytol 215:489–499

Trifilò P, Raimondo F, Lo Gullo MA, Barbera PM, Salleo S, Nardini A (2014) Relax and refill: xylem rehydration prior to hydraulic measurements favours embolism repair in stems and generates artificially low PLC values. Plant Cell Environ 37:2491–2499

Vaz M, Cochard H, Gazarini L, Graça J, Chaves MM, Pereira JS (2012) Cork oak (Quercus suber L.) seedlings acclimate to elevated CO_2 and water stress: photosynthesis, growth, wood anatomy and hydraulic conductivity. Trees 26:1145–1157

Vilagrosa A, Bellot J, Vallejo VR, Gil-Pelegrín E (2003) Cavitation, stomatal conductance, and leaf dieback in seedlings of two co-occurring Mediterranean shrubs during an intense drought. J Exp Bot 54:2015–2024

Wheeler JK, Sperry JS, Hacke UG, Hoang N (2005) Inter-vessel pitting and cavitation in woody Rosaceae and other vesselled plants: a basis for a safety versus efficiency trade-off in xylem transport. Plant Cell Environ 28:800–812

Wong SC, Cowan IR, Farquhar GD (1979) Stomatal conductance correlates with photosynthetic capacity. Nature 282:424–426