Commentary

The vulnerability to drought-induced embolism-conduit diameter link: breaching the anatomy-physiology divide

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Summary – The best explanations of the relationship between organismal form and function-those regarded by scientists as the most solid — always account for both comparative, across-species, patterns, as well as experimental results. This is true in all of biology, as it is for the study of xylem structure-function relations, where there is still a need for xylem physiology and functional comparative wood anatomy to mutually complement each other. To illustrate the magnitude and urgency of this need, we discuss Sherwin Carlquist's postulate of a link between vulnerability to drought-induced embolism and conduit diameter, summarizing some of the major global patterns of xylem trait variation that are currently explained by postulating a vulnerability–diameter link. These include wider community mean and maximum vessel diameters in wetter vs drier vegetation types; that vessels can be >700 μm in diameter but plants virtually always produce much narrower ones; that dryland plants with wider vessels drop their leaves earlier; wide-to-narrow vessels across growth rings; and the wide vessels of lianas surrounded by narrow vessels. These patterns are global, and we are aware of no anatomical evidence contradicting a vulnerability–diameter link. Despite the pervasiveness of these patterns, many xylem biologists do not regard the patterns as providing guidance for research in functional xylem biology. Instead, proposing and testing hypotheses to account for all of the data — xylem physiology experiments and comparative anatomical patterns in all their complexity and with all of their contradictions — provides the best way forward for the field. This effort requires proposing and testing hypotheses that are consistent with both experimental as well as comparative data. Crucially, it also requires not rejecting the vulnerability–diameter link without providing an alternative explanation that better explains the patterns currently explained by appeal to the link.

Keywords – Adaptation, drought-induced embolism, natural selection, vulnerability–diameter link, xylem evolution, xylem vulnerability to embolism.

Principles for good xylem science

A scientific principle so basic that it has been called the "First Law of Scientific Change" is that a scientific explanation is not rejected until it can be replaced by a better one (Barseghyan 2015). This principle is the "first law" because science cannot proceed through pure rejection. There will always be some data that are inconsistent with any theory, some data points unaccounted for by a hypothesis, and some exceptions to a rule, that can provide some scientists with a basis for rejection of a given explanation (Psyllos & Curd 2010). In one important example, such

ambiguity is manipulated to a pernicious effect by those who deny the anthropic contribution to climate change (Dietrich & Skipper 2007; Turnbull 2018; Andersen & Rocca 2020). It is always possible to point to some inconsistent result or some missing datum and reject a theory because "all of the data are not in yet". The principle of "reject any explanation when faced with any inconsistency" is part of what has been called radical empiricism (Nelson 1970). "Radical" in this sense denotes "to the root", and the radical empiricist position is that scientific truth emerges largely unaided from the accumulation of neutral facts, with a minimal role for "speculation". The contrasting position is hypothetico-deductive science, in which scientists propose hypotheses that attempt to explain as much of the data as possible, and iteratively test, reject, and refine these hypotheses. Under hypothetico-deductive science, hypotheses are the indispensable and fundamental guides to exploring the natural world. Because there will always be some inconsistencies and unknowns, under radical empiricism, we would be left with a world in which as scientists we can only say that the world is very complicated, and we haven't figured it all out yet. Instead, scientists must develop potential explanations — theories, hypotheses, models[1] — for the most salient and consequential patterns in nature, and subject them to testing and refinement (Ladyman 2002).

The true scientific standard for choosing explanations is to fit the data and explanatory power, not total absence of inconsistencies, and this principle offers helpful guidance for functional xylem biology. There is always a vast pool of potential explanations for any given set of data or patterns in nature. The explanation or explanations that best fit the data at any given time are the working explanations. Because any explanation or theory will always have inconsistencies, demanding total absence of inconsistencies for accepting a theory leaves science without theories. Moreover, radical empiricists tend to draw a much wider line around ideas as being unfounded and untestable "speculation," often dismissing ideas that hypothetico-deductivists see as appropriately grounded and empirically accessible scientific theory. Where scientists trace these lines is important because absence of theory leads to a lack of direction in science. It's impossible to distinguish high priorities for empirical investigation from low ones without a guiding theory (Mayr 1982). Recognizing that there will always be frontiers to knowledge requires identifying the explanation that best fits the data and using that one (or ones) as the working explanation. Scientists can then identify the outstanding questions that emerge as they study the fit between the working theory and the data and thus proceed in a directed and efficient manner to develop better and better working pictures of the natural world. Science is thus a process of inference to the best explanation (Ladyman 2002).

Science as inference to the best explanation view lays out a clear vision of scientific progress. The daily work of scientists is to identify the best explanation given the data at any given time. Empirical unknowns and inconsistencies with that explanation spur further empirical investigation. Empirical investigation leads to new discoveries that allow the old explanation to be modified or replaced wholesale. Progress in science is thus replacement of one explanation for a new one that explains everything that the old explanation did plus additional phenomena. To impede progress in science, it is sufficient merely to reject the working explanation without replacing it. For science to flourish, the working explanation should be rejected only when scientists can provide a better alternative to replace it. Here, we describe a very important debate in functional xylem biology, one founded by Sherwin Carlquist, that we suggest can be guided in helpful directions by the First Law of Scientific Change.

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[1] With regard to the terminology we use, the goal of science is to produce explanations. Theories and hypotheses are potential explanations, and they include mechanisms, known and postulated. There is no meaningful distinction to be made between a theory and a hypothesis, so we use these terms interchangeably. In evolutionary explanations such as those used in functional xylem biology, complementary layers of direct evidence, historical assumptions, and the observed data and the mutual confirmation among them, make up the explanation (Olson & Arroyo-Santos 2015). Biologists can come up with many potential explanations, and the one or ones with the best mutual fits among evidence, pattern to be explained, and assumptions are the preferred ones.

The postulated link between vulnerability to drought-induced embolism and conduit diameter

The debate surrounds the putative link between vulnerability to drought induced embolism and xylem conduit diameter. Carlquist posited that, all else being equal, wider conduits are more vulnerable to drought-induced embolism than narrow ones (Carlquist 1966, 1975, 1977). He proposed this hypothesis to explain a large number of observations in xylem biology, some of which we will touch on here. He did not propose in any detail a causal mechanism that would account for why wider conduits should be more vulnerable to drought-induced embolism. Instead, his explanation could be translated as "X, Y, and Z data are explained well if there is some sort of causal connection between vulnerability to drought-induced embolism and conduit diameter." Such so-called abductive reasoning is universal in science (Olson & Arroyo-Santos 2015). Like Carlquist not knowing what the nature of a possible vulnerability–diameter link might be, Darwin did not know what the mechanisms of inheritance were. Darwin simply postulated that "if there is some mechanism of inheritance such that offspring tend to resemble the parents, then natural selection can occur."

If xylem biologists think that the patterns currently explained by the vulnerability–diameter hypothesis are real, i.e., not mere sampling error, then given the pervasiveness of these patterns, a central task of xylem functional biology must be to determine the cause of these patterns. However, a current practice of some authors is to find inconsistencies with this hypothesis and simply reject it, without providing an alternative that accounts for the data. This radical empiricism leaves the field not only unable to explain some of the most important patterns in all of comparative wood anatomy but with little direction for further research.

Even more seriously, it means that functional xylem biologists are not providing crucial insight as climate change induced drought kills trees worldwide. Millions of trees are being lost to climate-change induced drought, with catastrophic consequences for biodiversity loss and nature's contributions to humanity. These mortality events involve multiple causes, but among these causes is failure of the hydraulic system, embolism in the face of drought (Davis *et al.* 2002; Pratt *et al.* 2014; Allen *et al.* 2015; Anderegg *et al.* 2015, 2016; Venturas *et al.* 2016a; Adams *et al.* 2017; Trugman *et al.* 2021). As a result, it is urgently incumbent on functional xylem biologists to develop a working theory of the connection between vulnerability to drought induced embolism and xylem structure. A key aspect of this process is providing an explanation to account for the patterns described below that are currently explained by the vulnerability–diameter link. Best-guess diagnostics are urgently needed to identify particularly vulnerable species or individuals, to intervene in rendering priority individuals more resistant to drought, and develop more drought-resistant varieties of cultivated trees, and this needs to be accomplished as soon as possible (Anfodillo & Olson 2021). To fulfill this pressing obligation to society, xylem functional biology must abandon radical empiricism and put itself firmly on a path of scientific progress. Doing so requires identifying the priority phenomena that require explanation.

Throwing down a (friendly but urgent) gauntlet to those who reject the vulnerability–diameter link: explain the following

The drought induced embolism vulnerability-conduit diameter link simultaneously and parsimoniously explains a very large number of xylem structure-function relations spanning the entire globe and, to our knowledge, essentially all species that have been studied. Because these patterns are globally pervasive and because, if there is a mechanistic link between vulnerability to drought induced embolism and conduit diameter, it promises to offer tools to manage forest mortality (Anfodillo & Olson 2021), it is the obligation and responsibility of functional xylem biologists to explain them. Those rejecting the vulnerability–diameter link must provide an alternative explanation that accounts for all of the phenomena currently explained by the link.

We now turn to some of these phenomena that require explanation. For the purpose of simplicity, we restrict our thinking to frost free habitats. In generating potential explanations, this allows us to remove the effect of adaptation

to cold (Ball *et al.* 2006; Sevanto *et al.* 2012). It is clear that adaptation to drought and to cold interact with one another. But for the purpose of exploring these patterns, as a starting point, we restrict the discussion to species that evolved in and inhabit frost-free habitats. In what follows, the "vulnerability–diameter" link refers to the putative link between vulnerability to drought induced embolism and xylem conduit diameter, excluding freezing-induced embolism.

Wider community mean and maximum vessel diameters in wetter compared to drier vegetation types

The most important pattern in so-called ecological wood anatomy is the correlation between conduit diameter and water availability. This pattern is observed in all communities that have been studied all over the world and there are no real exceptions. The pattern consists of the following elements. Water availability varies across habitats, from deserts to rainforests. In dry habitats, community mean conduit diameters are much narrower than those in moist habitats. These differences in mean conduit diameter are caused by widening of the range of conduit diameters in moister habitats. The low end of the range remains the same across habitats. In moister habitats, the range and maximum diameters are wider, and so mean conduit diameter is wider in moister habitats.

This global pattern is accounted for by the vulnerability–diameter link. Narrower vessels are selected for in drier environments because they are more resistant to embolism formation. Regions with more precipitation allow wider vessel diameters, so, depending on ecological strategy, some species in these communities have wider vessels. In all communities there is a range of ecological strategies ("ecological strategies"=suites of traits favored by selection, see Castorena *et al.* 2022) such that plants with narrow vessels are present in all communities. Wide conduits, though, are only found in moist communities, because selection eliminates them, the argument goes, in dry communities by virtue of their vulnerability. The wide conduit-moist community/ narrow conduit-dry community pattern has been recovered all over the world and we are not aware of any exceptions (Baas 1982; Baas *et al.* 1983; Baas & Carlquist 1985; Carlquist & Hoekman 1985; Alves & Angyalossy-Alfonso 2000; De Micco & Aronne 2012; Olson *et al.* 2018).

The pervasiveness of this pattern identifies it as a central priority for explanation. One possibility is that the pattern is not real. Spurious patterns can result from improper sampling, sloppy measurements, or sheer sampling error. These possibilities seem entirely unlikely given that the pattern has been observed so many times and so clearly. If there is a priority for explanation in xylem functional biology, surely this is it.

Maximum conduit diameter

Another pattern that is currently explained by the drought induced embolism-conduit diameter link is that conduits are virtually always well below the maximum observed diameter. The widest conduits, vessels, can reach >700 µm in diameter, yet most xylem functional biologists have never seen vessels this wide. Those who reject the vulnerability–diameter link would have us believe that there is no functional penalty whatsoever to wider diameters. From the "no vulnerability–diameter link" point of view, given their great transport efficiency given carbon cost, then vessels >500 µm should be very common, but vessels are almost always well below this diameter. Coalescence of conduits from narrow terminal ones into few very wide ones proximally would be much more economical in carbon than multiple parallel narrow conduits ("furcation" McCulloh *et al.*, 2003, 2004, 2009; Gleason *et al.*, 2018) and so would be favored unless wide conduits were a disadvantage, as for their embolism vulnerability.

Moreover, in any given plant, there is a range of conduit diameters produced. The "wide conduits" tail of the distribution shows that conduits much wider than the mean are developmentally possible at that point in that particular stem. This observation suggests that any given stem could produce much wider mean vessel diameters than it does, readily testable with techniques such as mutagenesis, hormonal manipulation, or selective breeding (Conner *et al.* 2011; Johnson *et al.* 2018; Rodriguez-Zaccaro *et al.* 2021). That most vessel diameters are well below the developmental maximum is consistent with the notion that wider diameters are developmentally possible but

not favored by selection because of their vulnerability to embolism. Construction cost arguments cannot be invoked because a single wide conduit would cost much less to build than many narrow ones.

Some have suggested to us that it might be that narrow-stemmed plants do not produce wide vessels because there is some developmental linkage between vessel diameter and stem diameter. This possibility is rejected by lianas, which routinely produce very wide vessels in slender stems (Carlquist 1985a; Angyalossy *et al.* 2012, 2015; Olson *et al.* 2014; Rosell & Olson 2014). Similarly, distal roots far from the plant base also have very wide vessels for their diameter (Olson *et al.* 2021). So there is no reason to think that heretofore unidentified developmental factors limit vessel diameter to what is routinely observed in any self-supporting plant. If there is no link between vulnerability and conduit diameter, why do small plants not simply have one or two 500 μm vessels supplying their leaves? Why do plants always have an array of vessel diameters so far below their developmentally possible maxima? These questions are most plausibly answered by invoking natural selection in the context of a link between vulnerability and diameter. Given that few very wide conduits would cost so much less in terms of carbon for a given conductance, those who reject the vulnerability–diameter link are under a heavy burden to account for why conduits are usually so much narrower than their developmentally possible maxima.

Height limitation by drought across habitats

The relationship between plant height, conduit diameter, and water availability is explained by appeal to the embolism vulnerability-conduit diameter relationship (Olson *et al.* 2018; Fajardo *et al.* 2020; Anfodillo & Olson 2021; Chambers-Ostler *et al.* 2022). Because they are associated with less negative xylem pressures, moister conditions allow for greater conduit diameters, assuming that there is a link between drought-induced embolism and conduit diameter. At the same time, selection favors whole-plant conductive systems in which conduits are very narrow at the distal ends, where water leaves the xylem and enters the mesophyll. In circulatory systems in general, selection maximizes surface area of conduits per unit fluid volume. Whether they be gills, lungs, or terminal leaf veins, this maximization of surface area permits diffusion of water and gases into and out of the circulatory system. If conduits remained the same diameter along the entire conductive system, then resistance would rapidly accumulate and increases in leaf length and tree height would be accompanied by dramatic drops in conductance. Instead, conduits widen predictably with distance from the tip, in such a way that conductance is maintained at least constant with height growth (Koçillari *et al.* 2021) (we say "at least constant" because plants can experience increases in vapor pressure deficit with height growth, so conductance would actually *increase* per unit leaf area with height growth; Olson *et al.* 2020a).

There is therefore an intimate relationship between climate, conduit diameter, and plant height, which is explained by postulating a vulnerability–diameter relationship. Selection favoring the maintenance of conductance with height growth means that growing taller requires wider conduits. Dry conditions limit conduit diameter, given the vulnerability–diameter link, and therefore plant height (Chambers-Ostler *et al.* 2022). Moist conditions permit wider diameters, given the vulnerability–diameter link, and therefore permit taller maximum and community mean plant heights. Xylem biologists who reject the vulnerability–diameter link need to provide an alternative explanation for the pervasive global pattern of variation in plant height with water availability, currently explained via the vulnerability–diameter relation (Olson *et al.* 2018). Olson *et al.* (2021) provide an argument against scenarios such as Cabon *et al.* (2020) and Koch *et al.* (2004) in which passive drops in turgor with growth limit plant height.

Height differences between clones given moisture availability

Natural selection has favored plastic responses in plants that lead to a fit between conduit diameter, plant height, and climate even within clones of the same individual. Such a pattern is satisfactorily explained by a scenario such

as the following, which points to a vulnerability–diameter relationship. Through potentially varying mechanisms across species, plants detect the xylem pressures that they experience, and set their maximum conduit diameters accordingly in a plastic response (Chambers-Ostler *et al.* 2022). Because of the relationship between conduit diameter and height, different mean conduit diameters are associated with different heights. This plastic response can be seen in all wild habitats. A pine seed falling on the deep, moist soil of a narrow canyon will grow into a tall tree. A seed from the same cone falling in a crevice on the rocky canyon wall will remain small. If somehow transplanted to the rocky crevice, the tall plant would suffer catastrophic hydraulic failure. These plastic responses also operate across clones of the same species. A clone in a dry microsite (as in an infrequently watered pot) remains smaller, allowing it to produce the narrow vessels corresponding to the xylem pressures experienced; a clone in a wetter area experiences conditions allowing for wider vessels and consequently can grow taller (Keller & Tauer 1980; Devakumar *et al.* 1999; Cocozza *et al.* 2010; Chambers-Ostler *et al.* 2022). Variation in height across microsites is consistent with the expectation that plants cease growth at the height corresponding to the maximum conduit diameter permitted by the embolism risk of a given microsite. An explanation that rejects the link between drought induced embolism vulnerability and conduit diameter therefore needs to provide an alternative account of height limitation given water availability across clones of the same individual.

Preferential vulnerability of taller individuals

More and more studies find that the tallest individuals within a species or forest tend to be preferentially vulnerable to drought induced mortality (Bennett *et al.* 2015; Rowland *et al.* 2015; Meakem *et al.* 2018; Stovall *et al.* 2019). These studies do not assert that the largest individuals at any given site are always the most vulnerable or that it is impossible for a small plant to succumb to drought while a taller plant adjacent to it survives. Instead, the tendency for larger individuals to be more vulnerable is an aggregate pattern at a large scale (Trugman *et al.* 2021). It suggests that, if all else were equal, the taller individual subject to the same conditions would succumb to drought sooner than smaller individuals. This is an extremely consequential pattern that urgently demands explanation. Compared to smaller individuals, large trees produce disproportionately more propagules to a forest and sequester disproportionately more carbon (Enquist *et al.* 2020). The loss of a few large individuals thus drastically alters the genetic landscape of a forest and its ecosystem services, to say nothing of its cultural and aesthetic richness. Rather than radical empiricism, decisive and vigorous theory-construction is urgently needed to prevent the loss of more of the world's ancient trees.

Such a theory is provided by postulating a drought induced vulnerability-conduit diameter link (Anfodillo & Olson 2021). Taller individuals have predictably wider conduits. Given a vulnerability–diameter link, all else being equal, taller individuals should therefore on average be more vulnerable to drought induced embolism than shorter members of the same species in the same microsites. In stark contrast to a radical empiricist position, the vulnerability–diameter link provides clear guidance for identifying the most vulnerable individuals and provides clear direction for empirical research.

Crown dieback as an adaptation

Plants worldwide are experiencing death of terminal branches under drought (Davis *et al.* 2002; Camarero *et al.* 2015; Gonçalves Andrade Bueno *et al.* 2020). From the point of view of the vulnerability–diameter link, the ability to die back and resprout is seen as an adaptation to fluctuating conditions of water availability. Moist conditions permit wide maximum and mean conduit diameters because the upper limit on conduit diameter is wider when water is more plentiful and xylem pressures are, all else equal, less negative. Wider conduits are associated with taller plants. When conditions change and the climate becomes drier, the conduits that were appropriate to moister conditions are now excessively wide, in that they exceed the threshold of embolism vulnerability favored by selection in the focal

species. From the point of view of the vulnerability–diameter link, many plant species are seen to have an adaptive plastic response to such fluctuating conditions. When conditions become drier, plants must produce narrower, more embolism-resistant conduits. Because of the link between conduit diameter and plant height, production of narrower conduits must be accompanied by a reduction in total tip-to-base conductive pathlength. This reduction is achieved by shedding of terminal branches and resprouting at a shorter height. A shorter height means a shorter total tip-to-base conductive pathlength and therefore narrower conduits. Narrower conduits are more resistant to drought-induced embolism, and are therefore now appropriate to the current drier conditions (cf. Couvreur *et al.* 2018).

Branch shedding as an adaptation (cf. Rood *et al.* 2000) leading to narrower, more embolism-resistant conduits explains numerous observations that are otherwise impossible to account for without the vulnerability–diameter link (Kiorapostolou *et al.* 2020; Anfodillo & Olson 2021). One is the globally ever more frequent observation of terminal branch death and resprouting at lower heights, a pattern leading to shorter forests globally (Fajardo *et al.* 2019). Some taxa, such as oaks and eucalypts, include many species that shed terminal branches and resprout readily, whereas others do not (Zeppel *et al.* 2015). In addition to forest dieback, very old trees often show large dead snags in their crowns, signs of terminal death and resprouting associated with marked fluctuation in height over the centuries (Koch *et al.* 2004). Given the link between conduit diameter and plant height (Koçillari *et al.* 2021; Olson *et al.* 2021), such fluctuations in height would lead to adjustment of conduit diameter tracking water availability through fluctuation in climate. Upon more favorable conditions, plants can produce wider conduits again, leading to height growth. Which species do and do not exhibit shedding and resprouting, whether it is an adaptation or not, and whether the drought induced embolism vulnerability-conduit diameter link is involved or not are clear and important questions for empirical research (Zeppel *et al.* 2015; Anfodillo & Olson 2021). In any event, those rejecting the link between vulnerability to drought-induced embolism and conduit diameter need to provide an alternative explanation for such height fluctuations with water availability.

Wide-to-narrow conduits across growth rings

In frost-free, drought-prone areas, in plants in which vessel diameter varies markedly within growth rings, vessels in the earlywood are wider than in the latewood (Silva *et al.* 2019, 2021). Positing a link between vulnerability to drought-induced embolism and conduit diameter provides a compelling explanation for this pattern. In plants in drought-prone, frost-free areas, having narrow conduit diameters in the latewood is an obvious adaptive response to late season drought. In such plants, vessel diameter is "tuned" to the xylem pressures that the plant will experience as soil water potential becomes increasingly negative. In the early growing season, when water is abundant, water is drawn readily from the soil and xylem pressure potentials are not highly negative. These relatively moderate pressures allow for efficient conductance in wide, though vulnerable vessels. As water content in the soil wanes, the wide vessels tend to embolize, while the narrow latewood vessels tend to remain functional into the dry season. Narrower conduits are plausibly more resistant to drought-induced embolism. If so, then the production of narrower vessels in anticipation of drier conditions ensures that some conduits will remain functional even as conditions become drier and xylem potentials become more negative, maintaining water supply and photosynthetic productivity as high as possible given embolism risk. In this way, the margin between observed maximum transpiration rate per unit leaf area and theoretical maximum transpiration rate likely remains relatively constant as water availability wanes (cf. Couvreur *et al.* 2018).

Some authors propose that somehow passive (i.e., unavoidable and non-adaptive) drops in cell expansion ability with drops in water potential explain changes in conduit diameter across growth rings (Cabon *et al.* 2020; Chambers-Ostler *et al.* 2022; Lens *et al.* 2022), but this seems implausible. For starters, it posits that developmentally possible xylem cell diameter is limited by soil water potential. Therefore, the widest cells produced at any given moment are the widest ones possible given soil water potential. Because cell diameter is not under the control of the plant,

the fact that vessel diameters are finely regulated in such a way that they maximize conductance given embolism risk for prevailing conditions, and that they continue to meet leaf transpirational demands, is utter coincidence. Second, the notion that maximum conduit diameter is imposed by soil water potential makes numerous predictions that are readily tested. For example, we think we have observed latewood vessels in frost-free dryland habitats being formed early in the wet season, in multiple species. This observation requires formal exploration but would falsify the notion of passive drops in vessel diameter with soil water potential and supports the notion that vessel diameter is an adaptive feature in the context of water availability. Moreover, in our selection experiments (Alberto Echeverría *et al.* data not shown), we have bred lines of trees with vessels much wider than those typically observed in wild type populations, growing on the same soils and with the same moisture regimes as the wild types. If vessel diameter in the wild types were the sole consequence of soil water potential, it would be impossible to grow conspecifics with wider vessels on the same soil conditions. In warm dryland plants that produce multiple concentric growth rings and in which conduit diameter varies across the season, no exceptions to the wide-narrow trajectory are known. Surely this is a pattern demanding explanation at a very high priority among xylem scientists. The pattern is currently best explained by a link between vulnerability to drought-induced embolism and conduit diameter. Rejecting such a link leaves this pervasive pattern unexplained.

Leaf phenology and vessel diameter

Deciduous warm dryland plants that drop their leaves early in the dry season have relatively wide vessels, while co-occurring plants with relatively narrow vessels retain their leaves later into the dry season (Scholander *et al.* 1965; Kondoh *et al.* 2006; Méndez-Alonzo *et al.* 2013; Olson *et al.* 2020b; see also Vargas Gutierrez *et al.* 2022), another pattern that is intelligible given a link between vulnerability to drought induced embolism and conduit diameter. Given a vulnerability–diameter link, for a given water potential, plants that have wider vessels for a given plant height are more vulnerable to embolism. Leaf shedding is one way that plants avoid highly negative xylem pressures. Therefore, in species with relatively wide, and therefore vulnerable, vessels, selection favors early leaf shedding. Species with narrower vessels for a given height are more embolism resistant and therefore can retain their leaves later into the season. In this way, species with very different leaf phenologies, leaf masses per unit area, and vessel diameter given plant height coexist. This diversity of trait combinations is explained by postulating a link between vulnerability to drought induced embolism and conduit diameter in the context of leaf phenology. We are not aware of any alternative explanation ever having been proposed for this anatomy-phenology correlation and rejecting the vulnerability–diameter link makes it harder to explain rather than more intelligible.

Association between conduit sculpture and narrow conduits

Internal vessel sculpture, warts, and vestures are all features that are plausibly regarded as adaptations to drought. In many species, especially in cold habitats or drylands, including frost-free ones, conduits have some sort of internal "sculpture". In all species, internal conduit walls undulate and vary in thickness between the pits, where secondary wall material is absent, to the maximally thick areas in between pits. In species with sculpture, there are additional regularities superimposed on this basic pattern of variation in thickness. Often, such sculpture takes the form of fine, raised, spiral ramp-like helices of wall material that create a tracery along the inner conduit wall. Even more commonly, multiple pit apertures share a groove, creating coarse spiral sculpture. In species with vestured pits (Jansen *et al.* 2004; Medeiros *et al.* 2019), the protuberances found inside the pit chambers are often seen on the vessel interior as well. In many species, vessel interiors are coated with fine "warty" layers (Parham & Baird 1974; Ohtani *et al.* 1984b). These features can be found intergrading or in combination (Ohtani *et al.* 1984a). Carlquist (2001) provides an overview of these sculpture types.

In most lineages of plants, sculpture is much more common in drylands and cold habitats than in warm, moist ones, and this occurrence suggests that sculpture is favored by selection because it helps resist embolism. If it were not related at all to resistance of embolism, then it would be just as common in the rainforest as in the desert. Sculpture tends to be so fine, or in the case of grooves and warts, so discontinuous around the interior of the vessel, that their presence due to selection favoring avoidance of mechanical deformation of conduits under negative pressure seems unlikely. For example, the perforation plate in many cases seems likely to contribute to resisting deformation under negative pressure (see Echeverría *et al.* this issue). In this case, the annulus formed by the two adjacent perforation plates of abutting vessel elements is, in comparison with helical sculpture, quite massive. This massiveness seems more consistent with selection favoring mechanical resistance than it does in the case of internal conduit sculpture. In contrast, there is evidence that inner conduit wall sculpturing reduces contact angles of water with respect to the conduit walls. In practice, reduction of contact angles increases the "wettability" of the walls and thus decreases the likelihood of embolism (Kohonen 2006; Kohonen & Helland 2009; Lens *et al.* 2011). Whatever explanation turns out to be true, resistance to deformation, enhancing wettability, or some combination of the two, xylem biologists interpret internal conduit sculpture as an adaptation increasing resistance to drought-induced embolism.

For their part, vestures are also likely to represent adaptations to drought. Vestures are tubercular to coralliform projections found inside the pit chambers. In some cases, their dendritic structures fill the pit chambers such that the possibilities for deflection of the pit membrane are minimized. If deflection of the pit membrane increases the likelihood of passage of gas from embolized to active conduits (Hacke & Sperry 2001), then structures that minimize membrane deflection would be favored in conditions subject to highly negative xylem pressures (Zweypfennig 1978). In other cases, vestures are more like a frosting or coating of tubercles around the interior of the pit chamber or around the aperture. In these cases they seem unlikely to do much in the way of preventing deflection of the pit membrane, but perhaps contribute to wettability (Jansen *et al.* 2003). Consistent with these hypotheses are comparative patterns finding, as would be expected, that vesturing is more common in warm, dry areas as compared to moist, cold ones (Jansen *et al.* 2004; Medeiros *et al.* 2019). By all accounts, whatever their mode or modes of action, vestures are likely adaptations favored in resistance of drought-induced embolism.

When sculpturing, warts, or vestures vary within a growth ring, they are more pronounced in narrow latewood conduits (Parham & Baird 1974; Carlquist & Hoekman 1985; Carlquist 2001). This association makes sense if we postulate a link between vulnerability to drought-induced embolism and conduit diameter. For example, helical sculpture being an adaptation increasing resistance to drought-induced embolism is consistent with its preferential occurrence in latewood. In plants in warm drylands, once the rains dwindle and stop, soil and xylem water potentials become ever more negative. It is the latewood, which remains functional as the rainy season ends and the dry season sets it, that experiences the maximally negative pressures. As a result, preferential production of structures that help resist embolism is to be expected in latewood as compared to earlywood. If helical sculpture did not contribute to resisting embolism, then when there is variation between earlywood and latewood in the production of sculpture, it is not clear why it is produced in latewood and not earlywood. Similarly, if there is no causal connection at all, however indirect, between vulnerability to drought induced embolism and conduit diameter, then it is not clear why conduit diameter should vary across growth rings at all or why growth rings do not routinely proceed from narrow to wide from the wet to the dry season. In this way, it is most consistent with the data to invoke a link between vulnerability to drought induced embolism and conduit diameter and to view narrow conduits and internal sculpture and vesturing as members of a suite of embolism-resistant features in latewood.

Association between vasicentric tracheids and narrow conduits

An argument analogous to the previous one, on conduit sculpture and narrow conduits forming part of a drought-resistant suite of traits, also applies to presence of vasicentric and vascular tracheids (as defined by Carlquist 2001).

Vasicentric tracheids are conductive imperforate tracheary elements that occur adjacent to vessels in woods that bear, as their main imperforate tracheary element type, libriform fibers or fiber-tracheids, which are non-conductive (Carlquist 1985b, 1987; Barotto *et al.* 2016; Olson *et al.* 2020b). Vasicentric tracheids lack perforation plates and so embolisms are more likely to remain confined to single cells rather than propagating axially as they do in vessels. Because they surround vessels, they offer connectivity between vessels such that water can flow around embolized vessels and lower the possibility of air-seeding between vessels. If all the vessels embolize, vasicentric tracheids should retain some supply of water to the leaves or buds (Percolla *et al.* 2021; Pratt *et al.* 2015, 2020). They are common in frost-free drought-prone habitats, where they are regarded as adaptations to drought.

Vascular tracheids are also conductive imperforate tracheary elements found in woods that otherwise have (non-conductive) libriform fibers or fiber tracheids, but in contrast to vasicentric tracheids, which are found around vessels, vascular tracheids are found as the last layers of latewood, often in a continuous band, and without any vessels. Like vasicentric tracheids, vascular tracheids in plants of frost-free drylands are also regarded as adaptations to drought. By ending growth rings with imperforate elements and no vessels, a plant maximizes its conductive safety and maintains some intact water columns under the most highly negative conditions that the plant typically experiences. In plants of frost-free drylands, we are unaware of any other explanation for the presence and function of vasicentric and vascular tracheids except as adaptations to drought.

Having defined vasicentric and vascular tracheids as adaptations to drought, we can now develop the argument analogous to the previous one on internal vessel sculpture. When vasicentric tracheid abundance (which includes presence/absence) varies between earlywood and latewood, they are present or more abundant in the latewood, when they are associated with narrow vessels. At the same time, vascular tracheids are preceded by the production of narrow vessels. Both vasicentric and vascular tracheids are favored as highly embolism resistant conductive imperforate tracheary elements. That their areas of peak abundance coincide with or are adjacent to the narrowest vessels in a growth ring is consistent with narrow vessels also being resistant to embolism in the latewood.

Vessel diameter distribution skew

Some data suggest that species in arid environments have right-skewed vessel diameter distributions, while species from mesic environments have left-skewed vessel distributions (Hargrave *et al.* 1994; Pfautsch *et al.* 2016). Left- and right-skewed distributions of vessel diameter depart from normal distributions in ways that likely affect embolism resistance. As a result, diameter distribution is almost certainly an important target of natural selection (Woodcock 1989; Ewers *et al.* 1990; Mapfumo *et al.* 1994; Mauseth & Stevenson 2004; Twumasi *et al.* 2005; Medeiros & Pockman 2014; Rosell & Olson 2014; García-Cervigón *et al.* 2020). In right-skewed vessel diameter distributions, most vessels tend to the narrow end of the diameter distribution spectrum, with relatively few wide vessels. In contrast, in left-skewed vessel diameter distributions, most vessels tend to the wide end of the diameter distribution spectrum, with relatively few narrow vessels. In arid environments, the risk of drought-induced embolism is higher compared to mesic environments, resulting in proportionally more narrower vessels and less wider vessels (right-skewed vessel distributions) in the species from arid regions, and vice-versa for the mesic species (Pfautsch *et al.* 2016). Thus, selection favoring higher proportions of narrow, embolism-resistant vessels in dryland species, and higher proportions of wide, more vulnerable vessels in species of moist habitats, is explained by appeal to the vulnerability–diameter link. Once again, those rejecting the vulnerability–diameter link have not provided any alternative explanation for these patterns.

The tip-to-base gradient in conduit diameter

Conduit diameter closely tracks the tip-to-base gradient in xylem pressure, in a way that is expected given the vulnerability–diameter link. Xylem pressures are most highly negative at the distal extreme of the conductive stream, becoming less highly negative toward the base. At the same time, conduits are narrowest at the distal end of the xylem system and widen quickly toward the base (Lechthaler *et al.* 2020). This close tracking of xylem pressure and conduit diameter is consistent with the action of selection in the context of a tradeoff (Koçillari *et al.* 2021). In this tradeoff, one vector of natural selection is toward conduits that are as wide as possible. The lowest resistance to flow, and thus the highest conductance, would be achieved by conduits that are uniformly wide, as wide as possible, from their basal most point toward the tip. The other, and opposing, vector of natural selection is resistance to embolism via narrow conduits, assuming a vulnerability–diameter link. Therefore, natural selection should fine-tune conduit diameter along the entire conductive path such that diameters, and thus embolism risk are "just right" — wide enough that they maintain conductance constant with height growth, but not so wide that they expose the plant to excessive embolism risk. Those who reject the vulnerability–diameter need to provide a plausible alternative explanation for why conduits are so narrow distally instead of the much more conductively efficient configuration of being uniformly wide base-to-tip.

Similar patterns between vessel-bearing angiosperms and conifers

Despite their very different xylem structure, angiosperms and conifers show numerous similar patterns that are satisfactorily explained by postulating a vulnerability–diameter link. Most angiosperms conduct most of their water in vessels, which have pit membranes with a relatively homogeneous structure. Even in tracheid-bearing angiosperms, the pit membranes are homogeneous. Homogeneous here is not to suggest that there is no variation from the center of angiosperm pit membranes to their peripheries (Li *et al.* 2016; Zhang *et al.* 2020; Kaack *et al.* 2021), but to contrast it with the torus-margo structure of many conifers. In angiosperms, passage of embolisms between conduits is resisted by the pit membrane, with its intricate network of channels. In many conifers, however, passage between tracheids is blocked by aspiration of torus-margo pits, acting as tiny valves (Jacobsen 2021). If pit membrane thickness were the main explanation for embolism resistance (Li *et al.* 2016; Lens *et al.* 2022), then angiosperms and conifers should show markedly differing correlations between conduit diameter and water availability.

Instead, despite their differing structures, conifers and angiosperms show similar drought responses in many aspects. For one, conifers in ever-moist frost-free localities lack the wide-to-narrow growth rings of conifers in seasonally cold or dry habitats (Carlquist 2017). It is sometimes argued that conifers produce marked growth rings as a division of labor between conductive earlywood and mechanical support latewood. If this were exclusively the case, then such rings should always appear in large tropical rainforest conifers, but they do not (e.g., *Araucaria subulata*, *Dacrydium balansae*). Wide-to-narrow growth rings are always found in dryland conifers, even small ones with little need for extensive mechanical support. Instead, just as in angiosperm growth rings, it is plausible that the wide-to-narrow tracheid pattern found in conifers in drought-prone areas involves selection favoring narrower tracheid diameters because they are more resistant to drought. By the same token, patterns of dieback and resprouting with climate fluctuations are similar in both angiosperms and conifers (Koch *et al.* 2004). Given that greater height requires wider conduit diameters in both angiosperms and conifers (Koçillari *et al.* 2021), dieback and resprouting shorter would make both angiosperm and conifer individuals more drought resistant by virtue of narrower conduits. In both conifers and angiosperms, taller individuals, with their wider conduits, are predictably more vulnerable to embolism (Olson *et al.* 2018). Similarly, both angiosperms and conifers have similar maximum absolute heights, consistent with height being limited by maximum conduit diameter due to embolism vulnerability. Some current authors attribute embolism resistance to pit membrane thickness, but given similar patterns of variation in height across climates,

dieback and resprouting, wide-to-narrow growth rings, and other key patterns, some features common to conifers and angiosperms must underlie these similar responses. Their very different pit membrane structures mean that the common feature between conifers and angiosperm cannot be pit membrane structure. Conduit diameter, with its potential link to embolism vulnerability, is a prime alternative candidate.

Vessel diameter variance in lianas

Lianas have wider vessel diameter variances than self-supporting plants (Carlquist 1985a; Ewers *et al.* 1997; Angyalossy *et al.* 2012, 2015; Rosell & Olson 2014), a pattern consistent with the vulnerability–diameter link. Lianas are well known for supposedly having very wide vessels. Certainly, they have much wider vessels for a given stem diameter than self-supporting plants. However, when controlling for stem length, they have similar mean vessel diameters as self-supporting plants (Rosell & Olson 2014). What differs is vessel diameter variance. Lianas have a few slightly wider vessels for a given stem length than self-supporting plants. Less recognized is that they also have significantly narrower vessels for a given stem length than do self-supporting plants. This phenomenon is true for all known plant families, current and fossil, in which lianas have evolved (Burnham 2009; Angyalossy *et al.* 2015), a strong case of convergent evolution.

This distribution, which is especially noteworthy in lianas that lack true tracheids as an all-conductive background, makes sense in the light of the drought induced embolism vulnerability-vessel diameter link. Lianas must supply their crowns via much narrower xylem transectional areas as compared to self-supporting plants. In such a context, it is no surprise that selection would favor the production of wider maximum vessel diameters as compared to self-supporting plants. Given the scaling of conductance as the fourth power of vessel diameter, producing a vessel diameter distribution with a slightly longer tail at the wide end of the spectrum would dramatically increase conductance per unit xylem transectional area. However, if wider vessels are more vulnerable to embolism, then these exceptionally wide vessels would be expected to be highly vulnerable. In such a context, production of larger numbers of narrow vessels (relative to self-supporting plants) for a given stem length can be explained by appeal to a link between vulnerability to drought induced embolism and vessel diameter. Given the likelihood of embolization of the wide vessels sooner or later, production of narrow to very narrow vessels would provide alternative pathways of high embolism resistance, sufficient to keep leaves or growing tips alive through drought or injury. Carlquist (1985a, 153) wrote "Narrow vessels certainly confer considerable potential safety, and we should do well to emphasize not merely the wide vessels of vines, but the abundance of narrow ones". Positing a link between vulnerability to drought-induced embolism and conduit diameter shows why we should do so. We are unaware of a plausible alternative explanation for wide vessel diameter variance in lianas that does not invoke the vulnerability–diameter link.

The role of xylem biologists is to seek explanations for salient patterns in nature

If there is one mission of science, surely it is to account for the most salient and impactful phenomena in nature, a principle that provides essential guidance for xylem functional biology. The patterns currently explained by the vulnerability–diameter link are not only some of the most globally pervasive patterns in all of comparative xylem anatomy, but if there is a drought induced vulnerability–conduit diameter link, then it is also one of the most impactful phenomena in xylem biology because of its pivotal importance in plant evolution and in forest response to climate change. Figuring out how to explain the patterns currently accounted for by the link thus provides essential guidance for functional xylem biology in a context of vigorous scientific progress. The observations described above are pervasive, with no anatomical data contradicting the notion that wider vessels are less able to resist embolism. So, we are left with a pressing need to explain these global patterns. This effort requires bold theories.

A vision for functional xylem biology

Some xylem biologists provide examples of visionary theories for testing, inspired by the vulnerability–diameter link. One example is Martínez-Vilalta *et al.* (2002), in which the authors mathematize a postulated link between vulnerability and vessel diameter. They do so by postulating a relationship between vessel diameter and pit membrane features. In their 2002 model, they postulated that maximum membrane pore diameter should be wider in wider vessels. If wider membrane pores have higher propensities for passage of gas between vessels, then wider vessels having membranes that are more permissive of gas passage would provide an explanation for why wider vessels are more vulnerable to embolism. Occasional teratological pit membranes, that are exceptionally permissive might be key in embolism passage and gas diffusion (Guan *et al.* 2021; Plavcová *et al.* 2013). If wider vessels are more likely to have such teratological membranes, then such a relationship could explain at least part of a vulnerability–diameter link, as well as results consistent with such occasional teratologies (Jarbeau *et al.* 1995; Christman *et al.* 2009, 2012; Venturas *et al.* 2016b). The "pores" in intervessel pit membranes turn out not to be direct cylindrical channels perpendicular to the membrane but instead intricate networks of fine passages anastomosing through the membrane, with narrow constrictions imposing thresholds for gas passage (Kaack *et al.* 2021). While fascinating and important, these observations have no impact that we can see on Martínez-Vilalta *et al.*'s fundamental prediction that some correlation between vessel diameter and pit membrane characteristics could account for a vulnerability–diameter link. For example, recent work suggests that thicker intervessel pit membranes are associated with narrower pore constrictions, meaning that all else being equal, vessels with thicker membranes should be more resistant to embolism (Lens *et al.* 2022). Considering this idea, Martínez-Vilalta *et al.*'s prediction can be expressed as the expectation that wider vessels should, all else being equal, have thinner pit membranes, which would then explain the greater vulnerability of wider vessels.

The prediction that, all else being equal, wider vessels might have predictably thinner intervessel pit membranes has been little tested. For example, in the survey of Lens *et al.* (2022), the authors concluded that there was no relationship by plotting pit membrane thickness versus vessel diameter across multiple species, with data from leaves, stems, trunks, and roots. Measurements that are more clearly comparable would be desirable. For example, conduits in leaves can collapse and recover their shape, whereas conduits in the secondary xylem are rigid, meaning that the mechanisms of embolism resistance and recovery are likely different between primary and secondary xylem (Brodribb & Holbrook 2005; Zhang *et al.* 2014, 2016). Testing the expectation of a membrane thickness-vessel diameter relationship based on comparable samplings, for example from twigs alone, would maximize comparability by minimizing variation such as that between primary and secondary xylem. Because most measurements of vulnerability to embolism in the secondary xylem are carried out in twigs, focusing on twigs promises the easiest pairing of results to measurements of vulnerability. Moreover, to establish the relationship between vulnerability to drought induced embolism and secondary xylem structure, it seems essential to focus first on plants that evolved in and are adapted to frost-free habitats, yet most data to date are from temperate plants. For example, 97% of the species studied by Lens *et al.* (2022) were from the temperate zone. Presumably adaptations to cold are overlain on those to drought in temperate species, meaning that, with their cold adaptations and ancestries, temperate species are a noisy starting point for disentangling any vulnerability to drought induced embolism-conduit diameter link. Finally, a priority for testing the intervessel pit membrane-vessel diameter relationship is covering a wide range of vessel diameters. In the "stems" (∼twigs) category examined by Lens *et al.* (2022), their largest category, most of the species mean vessel diameters sampled (75%) fell between 15 and 30 μm in diameter. This small range highlights the very low functional diversity spanned by temperate species, and further underscores the importance of sampling from frost-free areas. Because conduit diameter changes very rapidly from the stem tip toward the base in twigs, and because leaf size strongly influences twig conduit diameter (Lechthaler *et al.* 2020; Olson *et al.* 2021), it is essential to collect data from standardized distances from the twig tip and using leaf length as a covariable. Spanning a great deal of functional diversity, such as wood density, will also be essential. Vessels with thicker walls tend to have thicker

pit membranes (Li *et al.* 2016). For a given vessel diameter, a very wide range of wall thicknesses can be observed (Echeverría *et al.* 2022). As a result, any intervessel pit membrane-vessel diameter relationship is likely to have a degree of variation about the Y-axis, and only including a wide range of functional diversity would allow identifying the causes of this variation (cf. Olson *et al.* 2020b). Given all of these outstanding considerations, the important prediction in the spirit of Martínez-Vilalta *et al.* (2002) of a potential relationship between intervessel pit membrane thickness and vessel diameter remains a priority for testing, and illustrates the property that clear theories have of providing direction for vigorous empirical science.

Another example is the bold postulate of Jacobsen and Pratt (this issue) that vulnerability curve shape is correlated with vessel diameter distributions. These authors build on the vulnerability–diameter link to, with one stroke, not only potentially dispel the controversy regarding r- versus S-shaped curves but show compelling evidence that variation in vulnerability curve shape is highly biologically relevant. A vulnerability curve is the plot of the drop in conductivity associated with increasingly negative xylem pressures. Discussion of vulnerability curve shape has mostly focused on whether the curves are r-shaped, i.e., show very marked drops in conductivity at relatively low (not highly negative) pressures followed by lower drops with increasingly negative pressures. S-shaped curves show relatively little drop in conductivity at relatively low (not highly negative) pressures, punctuated by a period of marked drops and then another period of relatively lower drops with increasingly negative pressures (Cai & Tyree 2010). A great deal of discussion has surrounded curve shape. Some r-shaped curves are regarded as diagnosing the open vessel artefact, involving test segments of stem that are shorter than many vessels. Short test segments exclude the vessel termini, which are membrane bound. Lacking membranes, vessels open at one or both ends give up their water very readily, giving the appearance of great vulnerability (Torres-Ruiz *et al.* 2017). Some authors think that all r-shaped curves are artefact. Others, ourselves included (Olson *et al.* 2018), have carefully used test segments longer than conduit lengths and still find r-shaped curves, suggesting that curve shape variation is not simply artefact.

Jacobsen and Pratt make the quite daring assertion that variation in curve shape likely reflects underlying variation in vessel diameter distribution. It is daring because on the one hand it makes many specific predictions that are highly testable empirically. Testable hypotheses are valuable because they permit rapid scientific progress. They also require the courage to make highly specific assertions that are potentially rejectable. The hypothesis of Jacobsen and Pratt is also daring because of its explanatory reach and importance. The r- versus S-shaped curve debate, to say nothing of that over the potential link between vulnerability and conduit diameter, have so far defied consensus in the field. Jacobsen and Pratt suggest that, far from artefact, variation in curve shape (when the open vessel artefact is obviated) reflect a very important biological signal. In doing so, they show that curve shape goes far beyond r- versus S-shapes, including not just the specific function that best describes a curve, but also the absolute level of vulnerability for a given xylem pressure. Invoking the vulnerability–diameter link, they argue that S-shaped curves are the result of vessel distributions that are relatively leptokurtic with low variances. In such distributions, most of the vessels are of similar diameters. As a result, there will be relatively few highly vulnerable ones and relatively few highly resistant ones, corresponding to the relatively flat initial and terminal phases of S-shaped curves. With most of the vessels being of similar diameter, they are of similar vulnerability, and therefore tend to embolize around the same time, hence the rapid decline in conductivity in the intermediate phase of S-shaped curves. In contrast, r-shaped curves are associated with left-skewed vessel distributions, in which there are relatively few narrow vessels and more wide ones. In such species, a preponderance of wide and therefore vulnerable vessels would lead to a rapid (and non-artefactual) drop in conductivity early on. Jacobsen and Pratt describe the way that other curve shapes plausibly derive from different vessel distributions. Their hypothesis is compelling because, if there is a link between vulnerability and conduit diameter, then it is almost certain that selection favors different diameter distributions in different selective contexts, from drylands to rainforests and from trees to lianas.

Martínez-Vilalta and Jacobsen and Pratt could turn out not be correct in all their postulates and predictions. No matter. What is important about their courageous work is that it sets out clear and unambiguous predictions for testing. Models whose parameters can be adjusted such that they can depict any situation are much less useful

than those that make very specific predictions. Hypotheses that make very specific predictions give bold direction to empirical work and provide the basis for interventions, such as those needed in the current situation of forest mortality. Along these lines, finding an explanation for the patterns described above represents a clear path for progress in functional xylem biology.

Xylem biologists: find an explanation for the patterns currently explained by the link

It is hard to overestimate the benefit to science and society that would accrue from identifying the causal mechanisms underlying the patterns described above. If there is a causal link between vulnerability to drought induced embolism and conduit diameter, what is it? If there is no link, and for all we know, there may not be one, then what accounts for all of the patterns above that are currently simultaneously and satisfyingly accounted for by the link? Whether there is or is not a link, discovering the causes of the patterns above promises to provide unprecedented insight into the factors that drive the evolution of plant hydraulic systems in the context of habit and habitat, and to provide the means for prediction and intervention in the current dire circumstance of climate change-induced forest mortality.

As anatomists whose purview it is to identify the most widespread patterns in xylem structure, we would like to close with a friendly but firm entreaty to our physiologist colleagues who remain skeptical of the usefulness of explaining the patterns mentioned above. If our mission as scientists is to explain the most significant patterns in nature, then the patterns summarized above should command the attention of the entire field of functional xylem biology. We suggest that the most profitable way forward for the field is to ask, "how do I square experimental results with an explanation of the most pervasive patterns of xylem structure and plant function at a global level?". In this way, anatomists and physiologists will finally work together, as they should, to produce novel explanations that account for everything currently accounted for by positing a vulnerability–diameter link, plus so much more, the fruit of long-overdue integration across perspectives in functional xylem science.

Acknowledgements

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