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Modeling 400 million years of plant hydraulics

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MODELING 400 MILLION YEARS OF PLANT HYDRAULICS

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ABSTRACT.—Mathematical models of fluid flow thorough plant stems permit quantitative assessment of plant ecology using anatomy alone, allowing extinct and extant plants to be measured against one another. Through this process, a series of patterns and observations about plant ecology and evolution can be made. First, many plants evolved high rates of water transport through the evolution of a diverse suite of anatomical adaptations over the last four hundred million years. Second, adaptations to increase hydraulic supply to leaves tend to precede, in evolutionary time, adaptations to increase the safety margin of plant water transport. Third, anatomical breakthroughs in water transport function tend to occur in step with ecological breakthroughs, including the appearance of leaves during the Devonian, the evolution of high leaf areas in early seed plants during the Carboniferous, and the early radiation of flowering plants during the Cretaceous. Quantitative assessment of plant function not only opens up the plant fossil record to ecological comparison, but also provides data that can be used to model fluxes and dynamics of past ecosystems that are rooted in individual plant anatomy.

INTRODUCTION

The biophysical nature of plant physiology means that functional and ecological insights can be derived from plant anatomy and morphology. More than one hundred and fifty years of work on living and fossil plants (Brongniart, 1828; Bailey and Sinnott, 1915; Bailey and Sinnott, 1916) has aimed to understand not only the environments these plants inhabited (Arens et al., 2000; Beerling and Royer, 2002a, b; Kohn and Thiemens, 2010), but also the evolutionary trajectory of terrestrial plant function. Key aspects of plant physiology are determined by the physical properties of individual plant cells, and these dimensions can be preserved in the fossil record, opening up the evolutionary history of land plants' physiology to analysis. Recent work applying mathematical models to key plant tissues, namely water transport cells, has opened the door to quantitative understanding of the 400-million-year evolutionary history of vascular plants (Cichan 1986a; Wilson et al., 2008; Wilson and Knoll, 2010; Wilson and Fischer, 2011).

This review will: 1) summarize the state of knowledge on plant water transport; 2) describe the models used to quantify this aspect of plant performance; 3) outline some of the evolutionary patterns that result from application of these models to the fossil record; and 4) sketch out future directions and applications of plant physiological evolution.

Part 1: How do plants work?

At the core of terrestrial plant metabolism are a series of tradeoffs that drive the radiation of plant form and function (Niklas, 1994, 1997). One of the most important tradeoffs is the loss of water (in the form of water vapor) in exchange for the acquisition of carbon dioxide from the atmosphere (Taiz and Zeiger, 2002). In order to acquire carbon dioxide as a substrate for photosynthesis, plants expose their water-rich interior tissues to the dry atmosphere, leaving plants at risk of lethal desiccation. Plants have evolved a series of tissues to transport water from the soil to the sites of gas exchange, collectively called xylem, along with a second system to deliver photosynthate from leaves throughout the rest of the plant, called phloem.

Xylem forms a network of hollow tubes from the roots to evaporative surfaces, and flow through xylem is driven by evaporation of water from cells in the interior of leaves. As water is evaporated from the cell walls, surface tension causes small menisci (radius of curvature: ~10 to 50 nm) to form between cellulose microfibrils (~20 nm in diameter). With increasing
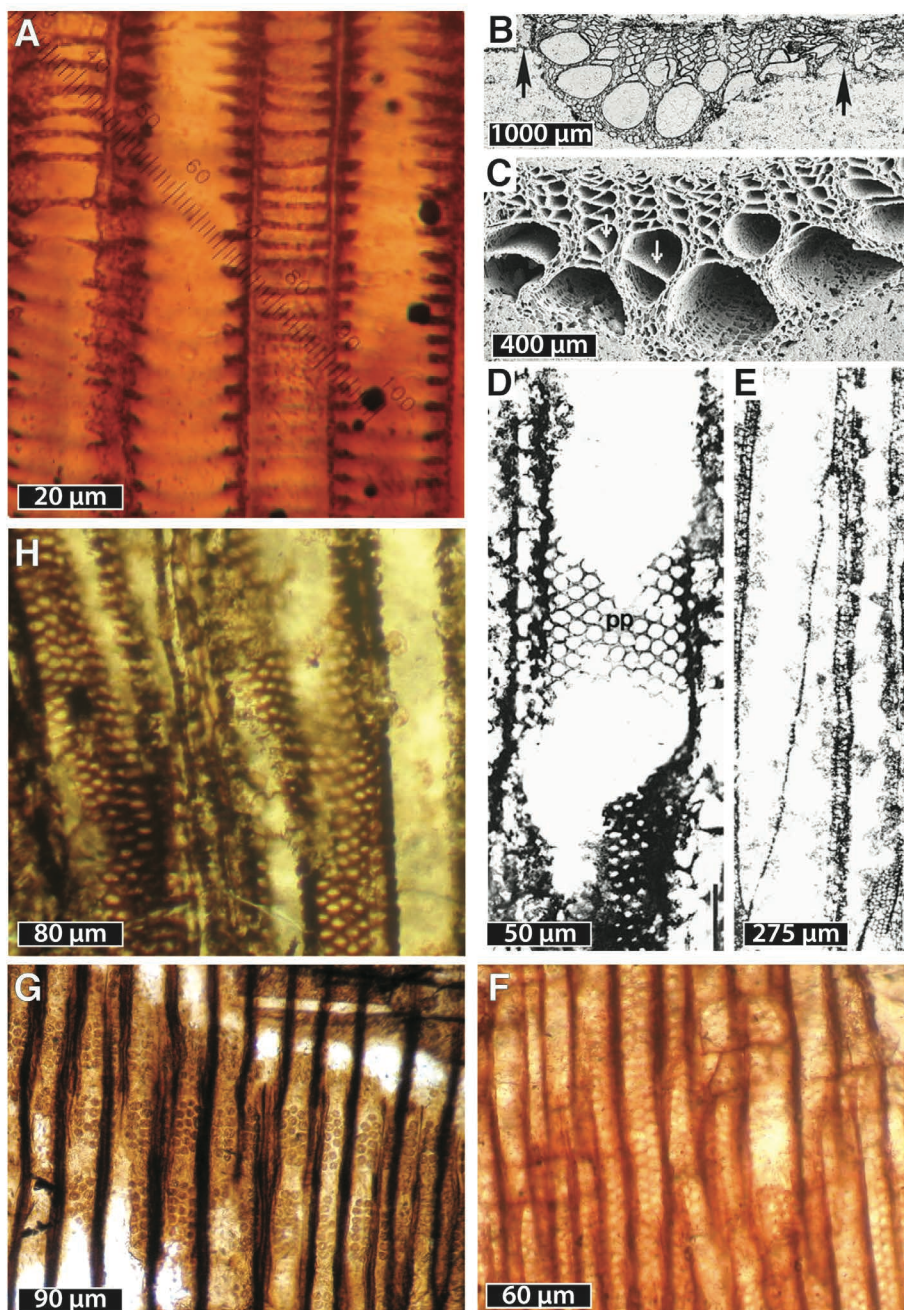

FIGURE *1*.—Detailed view of xylem anatomy and pit structure in Paleozoic plants. B–E modified from Li and Taylor (1999). A) Longitudinal section of xylem in the stem group lycophyte *Asteroxylon mackei* (Early Devonian, Rhynie Chert) showing annular thickenings, modeled using scalariform shapes in Wilson and Fischer (2011). B) Cross-section of a stem of the gigantopterid climbing plant *Vasovinea tianii* (late Permian, Xuanwei Formation), arrows indicate gaps that could be missing medullary rays; note the wide xylem vessels. C) Scanning electron micrograph of the specimen pictured in B); arrows indicate oblique endwalls, characteristic of vessels. D) A radial view of a vessel endwall in *Vasovinea tianii* showing a multiperforate perforation plate (pp). E) Tangential view of the perforation plate of a gigantopterid vessel; note enormous width of the gigantopterid vessel. F) Radial view of secondary xylem in *Cordaites* sp. (Pennsylvanian stem group conifer) showing clusters of circular-bordered pits and narrow tracheids. G) Radial view of clusters of circular-bordered pits on the secondary xylem of the progymnosperm *Callixylon newberryi* (Archaeopteridiales; Late Devonian). Specimen courtesy of Jean Galtier and Brigitte Meyer-Berthaud. H) Radial view of narrow tracheids in the stem group seed plant *Medullosa anglica* showing abundant circular-bordered pits (Pennsylvanian, Shuler Mine, Harvard University Paleobotanical Collection #24474).

evaporation, more water is lost from cell walls and the radius of curvature of the menisci decreases; the strong surface tension and hydrogen bonding of water molecules generates, in turn, a tension, or negative pressure, that draws water to the site of evaporation. This mechanism, combining evaporation, surface tension, hydrophobic cell wall compounds in xylem, and hydrogen bonding between water molecules, is described as the Cohesion-Tension Theory and results in the movement of water to the tops of the tallest trees without the expenditure of ATP (Dixon and Joly, 1895; Dixon, 1914; Zimmermann, 1983; Tyree and Sperry, 1988; Tyree and Ewers, 1991; Pockman et al., 1995; Sperry et al., 1996; Tyree and Zimmermann, 2002; Wheeler and Stroock, 2008). Xylem efficiency can be assessed with economic comparisons: all costs to the plant are involved with construction and maintenance, so if these costs are equal, then the highest flow rate is the most efficient.

As a result of the passive nature of water transport in xylem, the anatomy and structure of xylem cells determine the relative ease or difficulty of water transport through plants. That is, the dimensions, frequency, orientation, and morphology of transport cells determine the resistance to flow that water experiences on its way through a plant: the driving force, evaporation from the leaves, will vary throughout the day, but the hydraulic architecture of the transport system remains constant. Therefore, assessing the hydraulic resistance of the vascular system yields insight into the ecological and physiological characteristics of a plant independent of environmental variation. This method can be particularly useful in deep time, when even the most basic environmental parameters (e.g., atmospheric CO_2 concentration) can be underdetermined (Royer, 2006).

Among vascular plants, xylem cells fall into one of two broad categories: single-celled tracheids, typically found in lycophytes (Fig. 1A), ferns, and gymnosperms (Fig. 1F–H); and multicellular vessels, formed from individual cells called vessel elements, which reach their peak of diversity in the angiosperms but have been discovered in extinct lineages (Fig. 1B–E). Both vessels and tracheids have a number of morphological features in common: they are dead, empty cells that are differentiated, in a developmental sense, from parenchyma procambial cells; both are roughly tube-shaped;

and both have a series of porous features on their lateral walls to permit water to move from one cell to another, called pits (Fig. 2C–F, H). However, vessels and tracheids typically have a dramatically different aspect ratio. Vessel elements range from ~20 to more than 500 microns in diameter, 0.5–2 mm long, and are open at the top and bottom, but, when stacked, form multicellular vessels that can be several meters long (Tyree and Ewers, 1991; Fisher et al., 2002). Tracheids, on the other hand, are usually 5–35 microns in diameter, 1–5 mm long, and closed at both ends, forming woody tissue that is composed of a large number of small, closed cells.

By employing vessels and tracheids to provide a low-resistance pathway to the leaves, the cohesion-tension system can be highly efficient. However, the cohesion-tension system of water transport has its drawbacks. The most pervasive drawback is the threat of a water column rupture. Because the column is under tension, it is metastable: mechanical failure, pathogen activity, excessive drought, or environmental disturbance can allow air to penetrate the exterior of a plant and enter the transpiration stream. When air bubbles enter the transpiration stream, or the water column breaks under extreme tension, air bubbles will expand and fill the conduit, blocking transport of water (Tyree and Sperry, 1989). The nucleation of an air bubble or its entry into a xylem cell is called cavitation, and the expansion of the air bubble to block the conduit is called embolization. Unless the plant grows new xylem cells or reverses the embolism, flow through that conduit will stop, photosynthesis will halt, and the plant will die.

A variety of observations have pointed toward pit membrane morphology, architecture, and frequency as key factors determining vulnerability to cavitation and embolism; one of the most compelling has been documenting differential cavitation vulnerability in plants with similar xylem cell sizes but different pits (Sperry et al., 2002, 2005, 2006, 2007; Wheeler et al., 2005; Hacke et al., 2006, 2007; Pittermann et al., 2006a, b). These observations have shown that cavitation vulnerability is more strongly determined by pit structure than by any other single factor. The standard pit membrane is a permeable sheet of cellulose microfibrils, a remnant of the primary cell wall between two developing xylem cells (Fig. 2C, D). This type of membrane is often called a homogeneous pit membrane, containing small pores between the cellulose microfibrils on
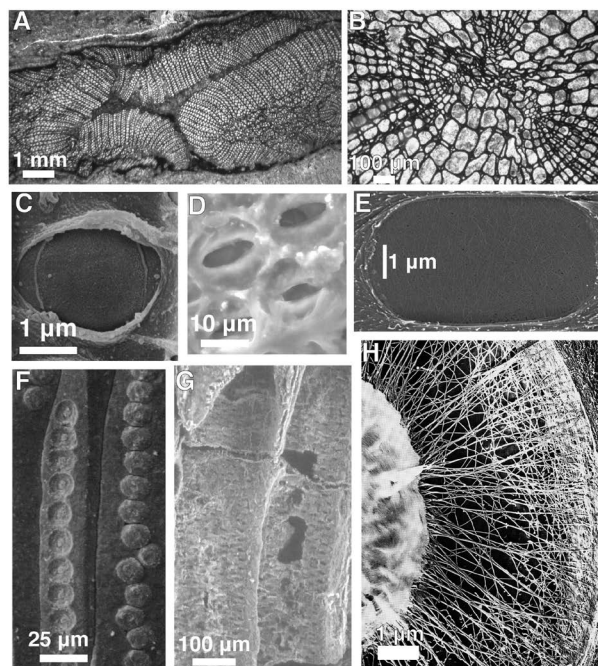
FIGURE 2.—Xylem anatomy of living and extinct plants. A) Cross-section of *Medullosa anglica*, showing extremely wide tracheids in the primary and secondary xylem (Pennsylvanian, Harvard University Paleobotanical Collection #7791). B) Cross-section of the sphenopsid *Sphenophyllum insignis* containing very large diameter tracheids and crushed primary xylem cells in the center (Pennsylvanian, HUPC #29234). C) A close-up view of a circular-bordered pit membrane from a fusainized tracheid of *Callixylon* sp. (Early Mississippian; modified from Beck et al., 1982). D) A radial view into pit membrane apertures of tracheids from *Medullosa* sp.; note the dramatic difference in size from the previous pit (Pennsylvanian, Shuler Mine). E) Radial view of an elliptical/scalariform pit from an extant vesselless angiosperm, *Trochodendron araloides* (modified from Hacke et al., 2007). F) Radial view of fusainized tracheids of *Callixylon* sp. (Early Mississippian) showing a single row of circular-bordered pits; this bears a close resemblance to the arrangement of pits in most extant conifers (modified from Beck et al., 1982). G) Radial view of macerated tracheids of *Medullosa* sp.; note the abundance of circular-bordered pits and the dimensions of the two cells (Pennsylvanian, Shuler Mine). H) Radial view of a torus-margo pit from the loblolly pine, *Pinus taeda* (modified from Côte, 1967).

the order of 5–40 nm in diameter (Choat et al., 2003, 2006; Choat and Pittermann, 2009). When the aperture around the pit is circular, the entire pit is called a circular-bordered pit (Fig. 2C, D); this is the most common pit morphology. When the aperture around the pit membrane is elliptically shaped, the pit is known as a

scalariform pit (Fig. 2E). These are found in a wide variety of spore-bearing plants, in the primary xylem of many seed plants, and on some angiosperm vessels. In some plants, the aperture remains circular, but the pit membrane differentiates into a thickened central portion and a very porous outer margin, known as the torus and margo, respectively (Fig. 2H). These torus-margo pits have the benefit of a high porosity because of the large pores in the margo (100–1000 nm in diameter), and a high safety margin, because the thickened torus can seal off the pit aperture in the event of embolism, acting as a valve to prevent the spread of air from one cell to another. The torus-margo pit is a key innovation within the conifer lineage and *Ginkgo*, and it appears to have evolved several times (Tyree and Sperry, 1989, 2003; Pittermann et al., 2005, 2006a; Sperry et al., 2006).

Until recently, embolism was thought to be irreversible, and damage from cavitation was thought to be mitigated by the production of new xylem cells (Zimmermann, 1983; Tyree and Sperry, 1989). However, a series of observations made over the last decade has shown that some plants possess the ability to refill embolized conduits when supplied with more water. In one experiment, MRI imaging of an actively transpiring stem of grapevine (*Vitis vinifera*) showed a reduction in the number of embolized vessels over a period of hours when the roots were supplied with additional water (Holbrook et al., 2001). Further investigation has shown that refilling is a dynamic process involving active transport of water from neighboring living cells into embolized conduits, suggesting that sugars and other solutes play key roles in this process (Holbrook et al., 2001; Clearwater and Goldstein, 2005; Brodersen et al., 2010; Secchi and Zwieniecki, 2011, 2012; Totzke et al., 2013). It appears that a high frequency of living cells within the xylem is a necessary precondition for embolism refilling, but it may not be a sufficient condition.

The great benefit of these plant physiological discoveries is that the 400 Ma paleontological record of fossil xylem can be subjected to quantitative analysis. Both xylem cell morphology (Fig. 2A, B) and pit membrane structure (Fig. 2C–E) can be preserved in the fossil record. From these dimensions, hydraulic resistance and ecological characteristics of extinct plants can be quantified. Earlier work focused exclusively on xylem cell length and diameter

(Niklas, 1985; Cichan, 1986a), but more recent work has included pit structure on the resistance side and cavitation resistance on the drawback side (Wilson et al., 2008; Wilson and Knoll, 2010; Wilson and Fischer, 2011).

Part 2: Quantifying flow rates

How can these key physiological parameters be quantified? Many of the quantitative observations of the effects of differential plant anatomy on transpiration rates were made by I. W. Bailey and colleagues during the 20th century (Bailey and Thompson, 1918; Bailey and Tupper, 1918; Bailey, 1953). The quantitative foundations for the mathematical model described here were laid by a variety of laboratories (Lancashire and Ennos, 2002; Hacke et al., 2004; Sperry and Hacke, 2004). Detailed descriptions of parameters and derivations can be found in previous work (Wilson et al., 2008; Wilson and Knoll, 2010; Wilson and Fischer, 2011).

The first quantitative breakthrough for mathematical modeling of hydraulic resistance, published by van den Honert (1948), applied the analogy of the flow of current through an electrical circuit of a defined electrical resistance to the flow of water through a plant with a defined hydraulic resistance. This relationship was expressed by using an analogy to Ohm's Law, in which the flow of current across a circuit (I) is defined by the electrostatic potential difference (ΔV) divided by the electrical resistance (R):

$$I = \Delta V / R \qquad \text{(Eq. 1)}$$

Using the Ohm's Law analogy, the flow of water through a plant (Q) is defined by the pressure drop across the plant (ΔP) divided by the hydraulic resistance (R):

$$Q = \Delta P / R \qquad \text{(Eq. 2)}$$

In this analogy, environmental variation (including relative humidity and temperature) has strong effects on the pressure gradient, which will change dramatically throughout the day. However, the hydraulic resistance is unchanging and is a function of anatomical properties of the xylem. This analogy could be applied to an entire plant (pressure drop from leaf to soil; equations summing up the hydraulic resistance of the entire path length from root to leaf), but to facilitate comparison between different plants, particularly fossil plants that may not be understood as entire organisms, this analysis is best done on a single-cell scale.

Looking at a single xylem cell allows the total hydraulic resistance (R_{tot}) to be deconvolved into two parts: hydraulic resistance from flow through the center of the xylem cell, the lumen (R_{lumen}), and hydraulic resistance from flow into and out of that cell through two sets of anatomical structures called pits (R_{pit}):

$$R_{tot} = R_{lumen} + 2 \, (R_{pit} / N_{pit}) \qquad \text{(Eq. 3)}$$

Xylem cells are approximately cylindrical in shape; therefore the hydraulic resistance of flow through the lumen can be approximated using the Hagen-Poiseuille equation, which is strongly determined by the diameter of the tube (D) but also includes parameters for tube length (L) and viscosity of water (v_{H2O}). Experimental studies have shown that the average molecule of water traverses half of the length of the cell before moving into the next cell, and substituting this distance (0.5 * L) for length into the standard Hagen-Poiseuille equation results in the following equation:

$$R_{lumen} = (64 \, v_{H2O} \, L) / \pi \, (D_{tracheid})^4 \qquad \text{(Eq. 4)}$$

Pit structure is more complex, with each xylem cell containing numerous pits and each pit containing two morphological features: an opening called an aperture and a porous sheet called a membrane. As described above, pit apertures and membranes vary dramatically across terrestrial plants, and three types are very common: circular-bordered pits (Fig. 2C, D), which have a roughly circular aperture surrounding a thin membrane; scalariform pits, which are more elliptical in plan view (Fig. 2E); and torus-margo pits, which have a circular aperture surrounding a membrane that has differentiated into an outer, porous portion (the margo) and an impermeable, inner portion (the torus) that can move back and forth and act as a valve (Fig. 2H).

Pits are modeled as resistors in parallel. That is, an increase in the number of pits (N_{pit}) yields a decrease in the total hydraulic resistance of that particular xylem cell: with more pits, water moves easily from one xylem cell to another (Eq. 3). In most vascular plants, two pits are aligned with one another in adjacent cells and water flows from one to another; these structures are called pit pairs. Each pit's hydraulic resistance has a
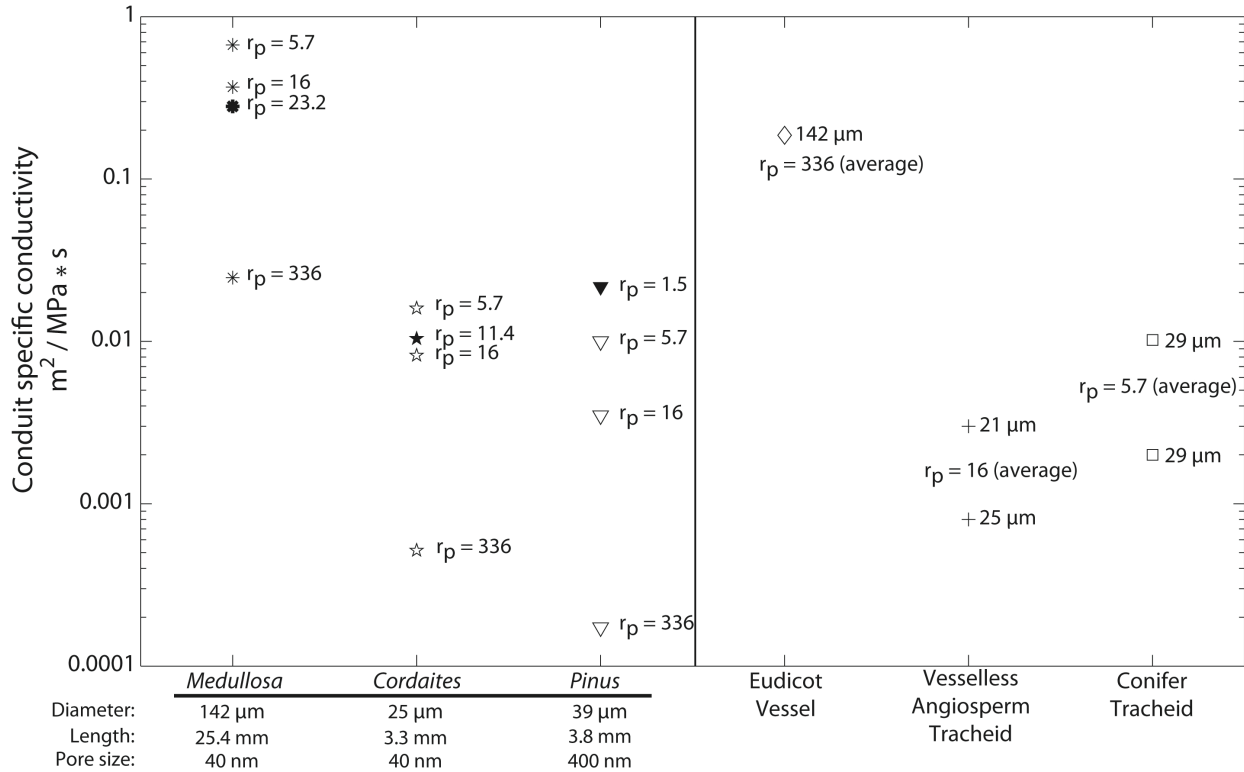
FIGURE *3*.—A quantitative comparison of living and extinct plant water transport capabilities using modeled (left panel) and experimental (right panel) hydraulics values, from Wilson et al. (2008). On the left are results from twelve model runs, four each from *Medullosa*, the stem group conifer *Cordaites*, and the living conifer *Pinus*. Each point represents a model run for conductivity of a single tracheid normalized to length and wall area of the cell (conduit-specific conductivity). At each point, a particular value for pit-area resistivity (pit resistance normalized to pit area; r_p) is substituted into the model, showing how different pit membrane porosities can be simulated; bold values are r_p values that satisfy the 80-20 (vessel) or 60-40 (tracheid) pit-lumen resistance partitioning. On the right are single-conduit values for hydraulic conductivity from an angiosperm vessel, a tracheid-bearing angiosperm that has secondarily lost vessels, and a conifer. r_p values are also pit resistance values; numbers are conduit diameters. Medullosan tracheids have substantial overlap with the hydraulic space that angiosperm vessels occupy.

component derived from each aperture of the pit pair, determined by aperture morphology ($R_{aperture}$), and another component derived from pit membrane morphology and porosity ($R_{membrane}$):

$$R_{pit} = R_{membrane} + 2 R_{aperture} \qquad \text{(Eq. 5)}$$

Pit apertures are modeled as short, cylindrical openings using a slightly modified Hagen-Poiseuille equation (compare with Eq. 4) that includes the aperture diameter (D_{ap}) and thickness (t_{ap}):

$$R_{aperture} = [128\, t_{ap}\, \nu_{H2O} / \pi\, (D_{ap})^4\,] + 24\, \nu_{H2O} / (Dap)^3 \qquad \text{(Eq. 6)}$$

Whereas pit membranes are modeled as thin, cylindrical sheets with pores of defined diameter (D_{pore}) and number (N_{pore}):

$$R_{membrane} = 24\, \nu_{H2O} / N_{pore}\, (D_{pore})^4 \qquad \text{(Eq. 7)}$$

Pit membrane porosity is among the most important parameters in this analysis. Pit membrane pores are very small: they are typically 5–20 nm in diameter for circular-bordered pits and scalariform pits, with pores infrequently reaching diameters in excess of 200 nm (Choat et al., 2003; Jansen et al., 2009), but can be more than 1 micron in diameter in torus-margo pits (Fig. 2H) (Côte, 1967). It is this difference in pit membrane pore size that allows conifers to match the hydraulic efficiency of angiosperms on a per-xylem-area basis (Pittermann et al., 2005, 2006, 2010).

Using this mathematical model, the contribution of pit membrane pores can be modeled using a variety of statistical distributions of pore sizes: normal distributions have been used

(Wilson et al., 2008), but substituting alternative distributions of sizes is trivial. A series of simulations of the effect of different pit membrane porosities based on different values of pore membrane diameters are shown for the stem-group seed plant *Medullosa*, the stem-group conifer *Cordaites*, and the living conifer *Pinus* in Figure 3. In the left panel, the hydraulic conductivity for tracheds from these three genera are shown, along with the effect of different pit membrane porosities (expressed as pit area resistance: pit resistance normalized to pit membrane area, or r_p) on the total hydraulic conductivity of each cell. As pits become less resistant, the hydraulic conductivity increases. When these modeled values are compared with hydraulic conductivity values derived from single-cell hydraulic resistance experiments on angiosperm vessels, conifer tracheids, and vesselless angiosperms (Fig. 3, right panel), medullosan tracheids are found to occupy the same hydraulic space as angiosperm vessels, and both *Pinus* and *Cordaites* closely overlap experimental values from conifer tracheids (Wilson et al., 2008).

In order to constrain values for pit membrane porosity, it is necessary to rely on guidelines derived from experimental data on living plants. When the proportion of hydraulic resistance coming from pits and pit membranes has been measured in living plants, small conduits (both tracheids and small vessels) have 54–60% of their hydraulic resistance arising from pits, whereas large conduits have 80–87% of their resistance arising from pit number and structure (Sperry et al., 2005; Wheeler et al., 2005; Choat et al., 2006). Xylem cells with large diameters have a lower R_{lumen}, increasing the other component of hydraulic resistance, that from pits and end walls. These relationships between lumen resistance and end-wall resistance can be used to evaluate and constrain parameters in these models, especially pit membrane porosity: in most plants, R_{lumen} would be expected to make up ~10–50% of the total hydraulic resistance, and pit membrane porosity can be adjusted accordingly.

When Equations 1 through 7 are examined, it should be clear that all of the terms used fall into one of four categories: 1) empirically measurable directly from fossilized material (e.g., $D_{tracheid}$, D_{ap}); 2) exhibiting limited but known environmental variation (e.g., v_{H2O}); 3) constants; or 4) spanning a range of sizes known from living specimens, but testable using sensitivity analysis

(e.g., D_{pore}). Taken together, a series of descriptive relationships emerge from these equations (Wilson and Knoll, 2010) as follows:

1) Wider cells have a lower hydraulic resistance and are more efficient.

2) Pit membrane resistance is the next most important parameter.

3) Length is the third-most important parameter as a linear term in the model.

Some useful dimensions and comparative hydraulic data can be found in Table 1.

Finally, the total hydraulic resistance (R_{tot}) can be expressed in a more intuitive form as its inverse, hydraulic conductance (K), which is simply the inverse of resistance. Hydraulic conductance can be normalized to any of several dimensions to yield hydraulic conductivity, including cell length, lumen area, pit area, or wall volume (Comstock and Sperry, 2000). Overall, low hydraulic resistance translates into high hydraulic conductance or conductivity, and vice versa.

Part 3: Quantifying drawbacks: cavitation and embolism resistance

The mechanism of cavitation and embolism points toward ways in which anatomical variation can be used to predict relative vulnerability. Low xylem pressure (or high tension) can draw air through pores in pit membranes, or around imperfectly sealed tori in conifer tracheids, pulling air into the transpiration stream (Cochard et al. 2009; Delzon et al. 2010). Therefore, in some way, pit-membrane pore diameter, along with the number of pits, size of pits, and/or dimensions of pit membrane area, should be predictive for embolism resistance (Hacke et al., 2001, 2007, 2007; Sperry et al., 2005; Wheeler et al., 2005; Pittermann et al., 2006a; Hacke and Jansen, 2009). Observations on living plants, both vessel-bearing and tracheid-bearing, largely bear out a relationship between increased pit area and increased cavitation vulnerability (Wheeler et al., 2005; Christman et al. 2012), but caution should be used when interpreting these estimates because there are uncertainties regarding the strength of these observations (Christman et al., 2009). Furthermore, statistical relationships based on one taxonomic group do not normally hold when applied to other taxonomic groups: high pit membrane area on a fern tracheid is much greater than high pit membrane area in a conifer tracheid.

The simplest method for calculating the likelihood of air-seeding and cavitation relies on

TABLE *1.*—Key physiological parameters and morphological features for extinct and extant plant xylem. Key references for measured values and ranges include: Diameter: Bailey and Tupper, 1918; Bannan, 1965. Length: Bailey and Tupper, 1918; Bannan, 1965. Pit Membrane Pore Diameter: Côte, 1967; Choat et al., 2004, 2008; Rabaey et al., 2006; Sano and Jansen, 2006; Jansen et al., 2007, 2009. Air-seeding Pressure: Sperry, 1986; Sperry and Tyree, 1988, 1990; Sperry et al., 1994, 2005, 2006, 2008; Hacke et al., 2000, 2001a; Hacke and Sperry, 2001; Pittermann and Sperry, 2003, 2006; Domec et al., 2006, 2008, 2009; Pittermann et al., 2006a; Johnson et al., 2013. Implosion Pressure: Hacke and Sperry, 2001; Hacke et al., 2001a; Sperry, 2003; Cochard et al., 2004; Domec et al., 2006, 2008, 2009; Johnson et al., 2013.

Name	Age	Diameter (µm)	Length (mm)	Pit membrane type	Pit membrane pore diameter (nm)	Air-seeding pressure (MPa)	Implosion pressure (MPa)
Angiosperm vessels	Extant	20–500	10–10,000	Homogeneous, scalariform or circular-bordered	5–40	-1 to -8	-3 to >-10
Vessel elements	Extant	20–500	0.5–2	Homogeneous, scalariform or circular-bordered	5–40		
Conifer tracheids	Extant	5–40	1–5	Torus-margo	100–1000	-1 to -7	-2.5 to >-10
Cordaites	~330–252 Ma (Mississippian to late Permian)	15–45	1.5–5	Homogeneous, circular-bordered	5–40	-4 to -7	-5 to -9
Medullosa	~330–295 Ma (Mississippian to early Permian)	30–250	10–30 (or more)	Homogeneous, circular-bordered	5–100	-0.8 to -2	-2 to -3
Asteroxylon	404 Ma (Early Devonian)	13–34	0.9–2.4	Homogeneous, scalariform to helical/annular ("G-type")	5–40	-2 to -5	-6 to -8

an equation for air passing through a pore in a membrane—in this case, for air passing through a pore in the pit membrane of a given size (typically 5–40 nm). The pressure gradient (ΔP) in MPa required to pull a bubble through a pore of a given diameter (D_{pore}) is a function of the surface tension of water (τ) and the contact angle between water and the pit membrane (θ; assumed to be 0°):

$$\Delta P = 4 \, (\tau \cos \theta / D_{pore}) \qquad \text{(Eq. 8)}$$

Substituting modeled pore dimensions allows the cavitation pressure of individual pit membranes (and therefore xylem cells) to be quantified.

Based on dimensions mentioned in the previous section, a pit membrane with uniformly distributed pores the size of those found in the margo of torus-margo pits (100–1000 nm) would be extremely vulnerable compared with those found in homogeneous pit membranes (5–20 nm, occasionally reaching 50 nm). However, in conifers and *Ginkgo biloba*, which bear torus-margo pits, the valve action of the torus, coupled with additional thickening of the margo fibers, prevents the spread of embolism, although repeated air-seeding events can increase the likelihood of a tear in the margo, allowing the torus to slip out of place—a phenomenon known as cavitation fatigue (Sperry and Tyree, 1988, 1990; Sperry and Sullivan, 1992; Hacke et al., 2001).

Along with pit membrane rupture and tearing,

another type of permanent, irreversible damage can occur: under extreme drought conditions, water-column tension can be so great that it collapses the xylem cells, leading not only to embolism but to conduit collapse (Hacke et al., 2001). Implosion is a common problem in biofuel crop strains that have been engineered to produce low amounts of the biopolymer lignin. In these plants, the xylem cells are not rigid enough to withstand the mechanical forces of a transpiration stream under extreme tension, and the cells collapse, cutting off the water supply to the leaves, with lethal results (Wagner et al., 2009). Implosion, therefore, is the extreme state of drought stress beyond cavitation and embolism, and quantifying implosion resistance permits robust estimates of a plant's physiological limits: they cannot be expected to live where their xylem would implode. Fortunately for paleobiologists, implosion pressure (I) is largely conveyed by the architecture of xylem cells themselves, specifically the square of the ratio of radial double-wall thickness (t) to the lumen diameter (b) of the xylem cell (Hacke et al., 2001). Cells with wide lumens and relatively thin walls are more vulnerable to implosion than cells with narrow lumens and thick walls, and statistical relationships have been derived through experimentally induced implosion (Hacke et al., 2001) (Table 1).

$$I = (t / b)^2 \qquad (Eq. 9)$$

Both lumen width and cell wall thickness are easy to measure in cross-sections of fossil plant wood, and these measurements yield important physiological results (Fig. 1).

One caveat should be added to this analysis: the vast majority of the experimental work on xylem function has been aimed at understanding vessel and tracheid function. Specifically, it has been aimed at understanding conduits with normal dimensions, and the statistical relationships derived from this experimental and modeling work is at its most accurate and precise when dealing with this portion of the parameter space. When dealing with unusual tracheid features (especially very high or low length or width and/or very high or low pit frequencies), an extreme result should be viewed as an indication that the particular xylem cell in question is outside of the statistical distribution defined by extant plants. For example, medullosan tracheids are so extreme in their length and width that they

have a very low value for R_{lumen}. When typical pit-membrane pore dimensions (5–20 nm) are used, the pits account for 98% or more of the hydraulic resistance of the cell. This is not out of the realm of possibility: the vessels within the American elm (*Ulmus americana*) have approximately 87% of their hydraulic resistance coming from pits (Choat et al., 2006). However, when choosing between model parameters, it is good practice to approach existing hydraulic allometries to as close a degree as possible. In the case of *Medullosa*, this means expanding the pit membrane pore size range to 5–100 nm to restore the lumen-pit balance to approximately 8 to 92%.

Part 4: Patterns and trends

When the fossil record of vascular plants is viewed through the lens of water transport, several observations and patterns come into focus. First and foremost, the angiosperm vessel and torus-margo pit in gymnosperms are key innovations, as other authors have noted over the last one hundred years (Bailey and Thompson, 1918; Bailey and Tupper, 1918; Bailey, 1953; Tyree and Ewers, 1991; Tyree and Zimmermann, 2002; Pittermann et al., 2005; Hacke et al., 2006, 2007; Sperry et al., 2006, 2007, 2008; Feild et al., 2009; Pittermann, 2010; Feild and Wilson, 2012). Both vessels and torus-margo pits dramatically reduce the hydraulic resistance in seed plants; torus-margo pits have the added advantage of providing increased safety through the action of their valves, so vessels can afford the increased hydraulic resistance and safety margin of homogeneous pit membranes (relative to torus-margo pits) because of their dramatically reduced lumen resistance. But, when vessels and torus-margo pits are placed into their evolutionary context, they are only two of the strategies that plants have explored to increase hydraulic efficiency. These other strategies are depicted stratigraphically in Figure 4, but can be broken down into three patterns.

Pattern 1: High hydraulic conductivity evolved many times.—The most obvious pattern that becomes clear when looking at the hydraulic capabilities of fossil plants is that plants have evolved many strategies to achieve high hydraulic conductivity (Fig. 4, red, pink, and orange bars). As described in previous work (Wilson and Knoll, 2010), there are a variety of extinct plants that achieved relatively high conductivity through either decreasing lumen resistance (i.e., developing larger conductive cell diameters) or
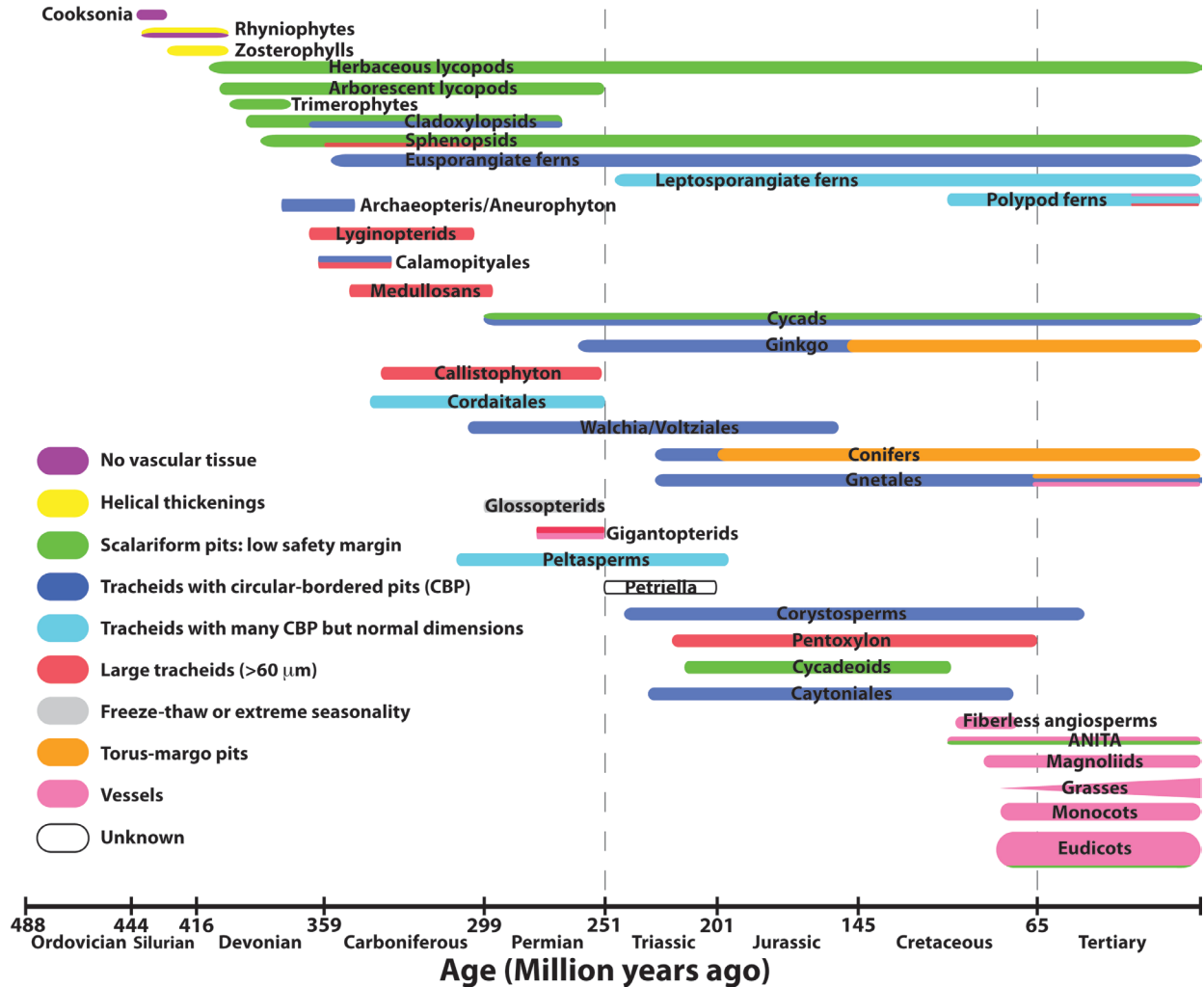
FIGURE *4*.—Stratigraphic ranges of plant groups coded for their hydraulic adaptations. Stratigraphic ranges and taxonomic names are from Taylor et al. (2008), with the exception of the fiberless angiosperms, used here to describe Early Cretaceous angiosperm flora of primarily small flowering plants that did not produce fibers from their vascular cambium (Philippe et al., 2008). ANITA corresponds to the eight basal angiosperm families (Amborellaceae, Nymphaeaceae, Illiciaceae, Trimeniaceae, Australbaileyaceae, Cabombaceae, Hydetellaceae, Schisandraceae). Colors represent some adaptations discussed in the text: scalariform pits, torus-margo pits, large tracheids, increased pit frequencies, and vessels. Large tracheids (red bars) are common in stem-group seed plant groups (*Medullosa, Lyginopteris, Callistophyton,* Calamopityales) and *Sphenophyllum* (red bar within sphenopsids); vessels (pink bars) evolve independently in the gigantopterids, the seed-plant group Gnetales, and in the roots of the polypod ferns (and possibly in other fern groups; Carlquist and Schneider, 2007); torus-margo pits (orange bars) evolve late within the conifer clade (and *Ginkgo*); scalariform pits (green bars) are the most common xylem type in spore-bearing plants. A vessel- and torus-margo-dominated world is a Cenozoic phenomenon.

decreasing wall resistance (i.e., adding more pits or decreasing the resistance of individual pits).

A number of extinct plants even pursued both strategies: evolving wide, long conduits with many pits. These plants tend to be smaller in stature, subcanopy or climbing, and have a moderate to high ratio of leaf-area to secondary-xylem area. These include the Paleozoic seed plants *Lyginopteris, Medullosa,* and *Callistophyton,* and the climbing sphenopsid *Sphenophyllum*; and the Mesozoic seed plant *Pentoxylon*. Each of these plant groups evolved tracheids more than 80 microns in diameter; *Medullosa* (Fig. 1H; 2A, D, G) and *Sphenophyllum* (Fig. 2B) contain both the longest and widest tracheids described to date in the fossil record, often exceeding 250 microns in diameter and 25 mm (2.5 cm) in length—roughly ten times

wider and longer than typical seed-plant tracheids (Andrews, 1940; Delevoryas, 1955; Cichan and Taylor, 1982; Cichan, 1985, 1986b, c; Wilson et al., 2008; Wilson and Knoll, 2010). Precisely how these two plant groups managed to develop cells of such extraordinary size is something of a developmental mystery, but unusual activity of the vascular cambium and a high degree of internodal elongation are likely to be the cause (Cichan, 1985, 1986b, c).

One consequence of the enormous tracheids found in *Medullosa* and *Sphenophyllum* is that these cells reach heights of hydraulic conductivity that terrestrial plants do not reach again until the evolution of angiosperm vessels during the Cretaceous (Feild and Wilson, 2012). Medullosan tracheids, in particular, are functionally indistinguishable from some crown-group angiosperm vessels (Wilson et al., 2008). Where these enormous tracheids diverge from angiosperm vessels, however, is in cavitation resistance: both medullosan tracheids (Wilson et al., 2008) and tracheids of *Sphenophyllum* (J. Wilson, unpublished data) are extraordinarily vulnerable to cavitation from their high pit area. The large lumens and relatively thin cell walls found within *Medullosa* and *Sphenophyllum* make them vulnerable to implosion at relatively modest tensions as well: the largest tracheids in each plant could implode at tensions as low as –2 MPa, a value temperate plants tolerate on a warm, dry, sunny day.

Large tracheids are extremely rare among living plants, with one reported occurrence in the climbing fern *Salpichlaena volubilis*, found in Central American tropical forests (Veres, 1990; Giudice et al., 2008; Luna et al., 2008). It is possible that other climbing ferns, including common genera such as *Gleichenia*, may include specimens with similarly wide or long tracheids—a number of authors have made similar observations in passing (e.g., Bliss, 1939).

Pattern 2: Safety last—An evolutionary pattern that is found in both seed plants and spore-bearing plants is that adaptations to increase hydraulic conductivity precede adaptations to increase water transport safety. Relatively evolutionarily early plants contain adaptations that maximize hydraulic conductivity and are replaced or succeeded by plants with safer xylem.

The most obvious example of this pattern comes from comparing extinct and extant conifers. Early conifers, including both stem-group conifers, such as *Cordaites* (Fig. 1F)*,* and

extinct members of crown-group conifer clades, all contain tracheids with a higher number of circular-bordered pits on their lateral walls than extant conifer species; all living conifer groups contain torus-margo pits instead (Fig. 4; blue and orange bars). In fact, the earliest torus-margo pit in conifers does not appear until the Hettangian (Early Jurassic, ~200 Ma) (Philippe and Bamford, 2008). When the cavitation vulnerability of these two adaptations is compared (multiple circular bordered pits vs. torus-margo pits), the stem-group conifers are more vulnerable to cavitation through the increase in pit area (Wilson and Knoll, 2010). To put it another way, ecologically successful conifer lineages with multiple circular bordered pits have all been replaced by ecologically successful conifer lineages with safer, fewer, higher-conductive torus-margo pits.

This pattern is also seen when looking at scalariform pits (Fig. 4, green bars). The earliest vascular plants contained a number of complex structures on their xylem cell walls, including some features that are so ambiguous that it is difficult to determine the degree to which these apertures were porous at all (Graham and Gray, 2001; Edwards, 2003). However, these early plants were succeeded by a number of vascular plants that contained tracheids with scalariform pits, which dramatically reduced the hydraulic resistance of their vascular system but acquired an increased risk of embolism. *Psilophyton dawsonii* from the Early to Middle Devonian Battery Point Formation on the Gaspé Peninsula, Canada, contains xylem that is largely pit area and small bars between pit membrane (Hartman and Banks, 1980). These cells bear a strong resemblance to xylem from some modern ferns and metaxylem of living seed plants, both of which are seldom long-lived tissues. Particularly in small ferns, aerial vegetative structures rarely persist more than a year, and in seed plants, metaxylem's functional role is usually taken over by secondary xylem, which tends to have a larger safety margin and is more stable and long-lived. *Psilophyton* is not singular: a number of other ancient lineages have scalariform pits of varying sizes, including the stem-group vascular plant *Renalia*, the ancestral fern *Rhacophyton*, and the arborescent lycophytes (Taylor et al., 2008). The early origin of scalariform pitting and large wall areas devoted to pit membranes implies an ecological strategy among early terrestrial plants that is focused on short-term gains: a 'live fast, die young' strategy

Pattern 3: Stem hydraulic adaptations radiate

in step with leaves and roots—Over the last several decades, it has become clear that anatomical revolutions have taken place within the terrestrial plant clade, including the evolution of secondary growth (Scheckler, 1978; Meyer-Berthaud et al., 2000), true rooting systems (Raven and Edwards, 2001), laminar leaves (Niklas, 1997), and the angiosperm leaf (Boyce et al., 2009). It has been noted that each of these transitions is associated with an increase in vascularization and/or hydraulic efficiency (Sperry, 2003), and single-cell analysis supports this view (Fig. 4). The radiation of new morphotypes and ecological strategies from the Late Devonian through the Pennsylvanian is accompanied by the evolution of large, efficient tracheids in stem-group seed plants and *Sphenophyllum*. Secondary xylem and the appearance of laminar leaves evolve in step with dense wood containing a number of circular-bordered pits, as shown in Figures 1 and 2. The large leaf areas of Carboniferous plants such as *Medullosa* are hydraulically maintained by the enormous tracheids found in stem-group seed plants. The advent of angiosperms brings the rise of angiosperm leaves along with vessels, and it is a curious coincidence that the torus-margo pit becomes the dominant pit structure in conifers at approximately the same time.

Part 5: Outputs and horizons

The utility of mathematical models of plant function is that informed estimates of plant physiological properties can be derived from fragmentary organs or disputed plants. For example, the calamopityales are a plant group known from permineralized, decorticated stems found in Mississippian rocks across North America and Europe, but leaves and reproductive structures have not been discovered in organic attachment to these stems (Rowe and Galtier, 1988; Speck and Rowe, 1994; Rowe et al., 2004; Decombeix et al., 2005; Galtier and Meyer-Berthaud, 2006; Decombeix et al., 2011a, b). Calamopityalean plants are thought to be stem-group seed plants because of the presence of xylem containing large rays, an arrangement that resembles other stem-group seed plants, including *Lyginopteris*, *Callistophyton*, and *Medullosa*, but until reproductive and foliar structures are discovered, our knowledge of the anatomy and phylogenetic position of these plants will remain limited. However, when the hydraulic resistance of these plants is calculated, a number of

calamopityalean species, including *Calamopitys embergeri* (J. Wilson, unpublished data), occupy the portion of the hydraulic morphospace later explored by these other high-conductivity stem group seed plants. Perhaps not surprisingly, biomechanical analysis (Rowe et al., 1993) and overall morphology (Galtier, 1970) of some of the calamopityaleans has pointed toward lianescent or non-self-supporting growth forms within this group, whereas other species, including *Calamopitys schweitzeri*, may represent intermediate hydraulic strategies between conifers and stem-group seed plants and may be self-supporting (J. Wilson, unpublished data; Galtier et al., 1993). Therefore, despite a limited window into the whole-plant structure and anatomy of the calamopityalean plants, inferences can be made regarding their physiology and ecology.

As another example, gigantopterids are an enigmatic group of plants known primarily from foliar compressions from the Permian across Asia and North America (Glasspool et al., 2004b; Taylor et al., 2008). Permineralized specimens are extremely rare, but demonstrate that some gigantopterids contained leaf venation comparable to that found in early angiosperms, along with vessels in stems (Li et al., 1996; Li and Taylor, 1998; Glasspool et al., 2004a, b; Boyce et al., 2009). Within the permineralized stems of gigantopterids, both vessels and tracheids can be seen (Fig. 1B, C), and vessels can be unambiguously distinguished by perforation plates in plan (Fig. 1D) and transverse views (Fig. 1E). Although insights into gigantopterid stem anatomy are limited because only a handful of fossils contain preserved internal anatomy, if any extinct plant were to occupy the physiological ecospace later taken by early angiosperms, the gigantopterids would be a strong candidate.

What may never be preserved?—Despite the ecological insight gained from mathematical modeling, key aspects of plant physiology may never be preserved in the fossil record. For example, embolism refilling appears to require that living cells and vulnerable xylem cells be in proximity so that living cells can pump solutes into embolized conduits and redissolve the air bubble under positive pressure (Clearwater and Clark, 2003; Secchi and Zwieniecki, 2011, 2012). Although there may not be a biochemical marker for embolism refilling capacity that is preservable over geologic time, the combination of vulnerable conduits next to living ray cells or axial parenchyma, with low amounts of secondary
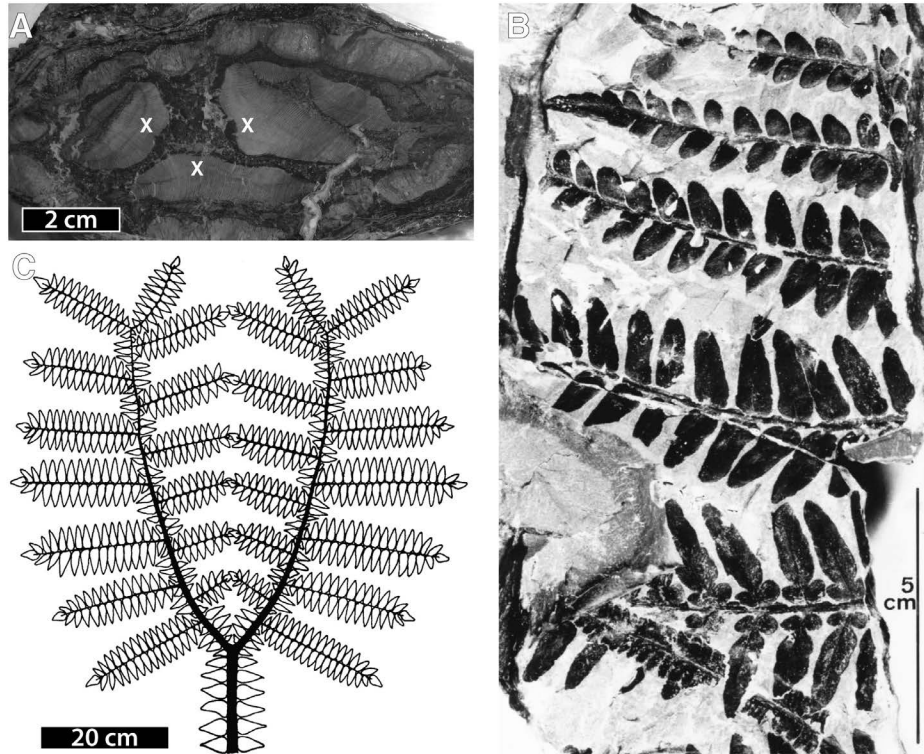
FIGURE 5.—Anatomy and morphology of *Macroneuropteris scheuchzeri*, a Pennsylvanian plant that presents a physiological puzzle. A) Transverse section of a *Medullosa noei* stem, thought to produce *M. scheuchzeri* fronds. Note three prominent xylem segments (each marked with a white x) in the center of the stem, surrounded by multiple layers of periderm. Specimen courtesy of Tom Phillips. B) *M. scheuchzeri* specimen from Nova Scotia showing heterophylly; from Zodrow (2003). C) Reconstruction of the frond architecture of a closely related species, *Macroneuropteris macrophylla*, showing the basal bifurcation characteristic of many medullosan fronds. It is highly likely that *M. scheuchzeri* fronds contained one more apical bifurcation. From Cleal et al. (1996).

xylem produced, may be read to imply refilling capacity in fossil plant stems. Both *Medullosa* and *Pentoxylon* meet these criteria, and some calamopityalean species may as well.

Why the disconnect between leaves and stems?—One of the puzzles among Paleozoic seed plants is that a number of plants suggested to have high hydraulic capacity also contain leaf features that are normally interpreted as xeromorphic: sunken stomata, a thick cuticle, and abundant trichomes on the leaves. For example, in the Pennsylvanian tropical forests of Pangea, the medullosan plant *Macroneuropteris scheuchzeri* (Fig. 5) contains these classic xeromorphic features, yet facies analysis (i.e., environmental reconstruction based on the sediments containing these fossils) shows that *Macroneuropteris scheuchzeri* occupied wetland environments, rather than drier environments (Stull et al., 2012). Furthermore, *M. scheuchzeri* leaves also contain structures interpreted as hydathodes, secretory tissues normally employed to excrete water from the margin of leaves, which are normally found in plants with access to an abundant water supply. As Stull et al. (2012) pointed out, how can a leaf contain both wet and dry features at the same time, and why might these leaves be attached to a low hydraulic resistance stem?

One possible way to reconcile this discrepancy involves leaf crown scaling: if stem-group seed plants, including medullosans, lacked some of the leaf-level features to maximize hydraulic efficiency seen in angiosperms, including high vein density and rapidly responding stomatal guard cells (Brodribb and Holbrook, 2004; Brodribb et al., 2005, 2007, 2010; Brodribb and Feild, 2010; de Boer et al., 2012), the massive leaf area found in many of these plants may have placed steep demands on the hydraulic supply by the stems. Stomatal guard cells that responded slowly to changes in light levels, temperature, soil water status, or humidity, as found in lycophytes and ferns (Brodribb and McAdam, 2011), may have led to high water loss

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from leaves, especially within plants that had a large leaf area with leaves that may have persisted over multiple years (Wnuk and Pfefferkorn, 1984; Stull et al., 2012). If medullosan stomata reacted to environmental stress as lycophytes and ferns do, rather than the way most seed plants respond (McAdam and Brodribb, 2012), hydathodes would be advantageous when soil moisture content was high, and the xeromorphic features would be advantageous when environmental conditions were dry. In effect, integrating slow stomata over a large leaf area may only have been possible with a low hydraulic resistance stem.

Simulating extinct ecosystems.—Finally, one of the most promising directions this research can take is to permit quantitative models of past and future ecosystems based on individual plant anatomy, including growth rates, water fluxes, and carbon fluxes (Medvigy et al., 2009, 2010; Hurtt et al., 2010; Ise and Moorcroft, 2010). Mesoscale ecosystem models have been used to model a variety of forest dynamics, from the hydrologic feedbacks that perpetuate cloud forests in Costa Rica to forest biomass dynamics under high-frequency environmental variation (Medvigy and Moorcroft, 2012). These models have contributed substantially to resolving differential spatial differences in predicted responses to anthropogenic climate change (e.g., Medvigy et al., 2010). Most of these models, including the Ecosystem Demography 2 model (ED2) (Moorcroft et al., 2001; Medvigy et al., 2009), include multiple vegetation types, each with its own biological properties, including growth rate, transpiration rate, and crown size. The major inputs to these models, therefore, can be resolved from analysis of fossil plants, and it should be possible to simulate past ecosystems, including variability within ecosystems. For example, ED2 could be run to simulate both a lycophyte-dominated swamp and a medullosan-dominated overbank ecosystem, and to explore their relative contributions to the hydrologic cycle and sensitivity to environmental conditions during the Pennsylvanian. Not only would this contribute to a more holistic understanding of these individual ecosystems, but these ecosystems can then be compared with modern analogues in a quantitative way.

CONCLUSIONS

Applying mathematical models to fossil plant material can provide a number of insights into evolutionary trends in land plants. It appears that early vascular plants prioritized low hydraulic resistance over safety from embolism, a pattern that is also seen within the conifer lineage. Although the angiosperm vessel is the ultimate low hydraulic resistance innovation among living plants, a number of extinct plants (both seed plants like *Medullosa* and at least one fern, *Sphenophyllum*) evolved comparably efficient xylem hundreds of millions of years before the evolution of angiosperms. Future work will build on these evolutionary patterns and will provide quantitative data that can be used to create accurate models of terrestrial ecosystems deep in the geologic past, enriching our understanding of the biological components of the Earth system.

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REFERENCES

ANDREWS, H. N., JR. 1940. On the stelar anatomy of the pteridosperms with particular reference to the secondary wood. Annals of the Missouri Botanical Garden, 27: 51–118.

ARENS, N. C., A. H. JAHREN, AND R. AMUNDSON. 2000. Can C3 plants faithfully record the carbon isotopic composition of atmospheric carbon dioxide? Paleobiology, 26: 137–164.

BAILEY, I. W. 1953. Evolution of the tracheary tissue of land plants. American Journal of Botany, 40: 4–8.

BAILEY, I. W., AND E. SINNOTT. 1915. A botanical index of Cretaceous and Tertiary climates. Science, 41: 831–834.

BAILEY, I. W., AND E. SINNOTT. 1916. The climatic distribution of certain types of angiosperm leaves. American Journal of Botany, 3: 24–39.

BAILEY, I. W., AND W. P. THOMPSON. 1918. Additional notes upon the angiosperms *Tetracentron*, *Trochodendron*, and *Drimys*, in which vessels are

absent from the wood. Annals of Botany, (Old Series) 32: 503–512.

BAILEY, I. W., AND W. W. TUPPER. 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.

BANNAN, M. W. 1965. Length tangential diameter and length/width ratio of conifer tracheids. Canadian Journal of Botany, 43: 967–984.

BECK, C. B., K. COY, AND R. SCHMID. 1982. Observations on the fine structure of *Callixylon* wood. American Journal of Botany, 69: 54–76.

BEERLING, D. J., AND D. L. ROYER. 2002a. Fossil plants as indicators of the Phanerozoic global carbon cycle. Annual Review of Earth and Planetary Sciences, 30: 527–556.

BEERLING, D. J., AND D. L. ROYER. 2002b. Reading a CO_2 signal from fossil stomata. New Phytologist, 153: 387–397.

BLISS, M. C. 1939. The tracheal elements in the ferns. American Journal of Botany, 26: 620–624.

BOYCE, C. K., T. J. BRODRIBB, T. S. FEILD, AND M. A. ZWIENIECKI. 2009. Angiosperm leaf vein evolution was physiologically and environmentally transformative. Proceedings of the Royal Society B: Biological Sciences, 276: 1771–1776.

BRODERSEN, C. R., A. J. MCELRONE, B. CHOAT, M. A. MATTHEWS, AND K. A. SHACKEL. 2010. The dynamics of embolism repair in xylem: in vivo visualizations using high-resolution computed tomography. Plant Physiology, 154: 1088–1095.

BRODRIBB, T. J., AND T. S. FEILD. 2010. Leaf hydraulic evolution led a surge in leaf photosynthetic capacity during early angiosperm diversification. Ecology Letters, 13: 175–183.

BRODRIBB, T. J., T. S. FEILD, AND G. J. JORDAN. 2007. Leaf maximum photosynthetic rate and venation are linked by hydraulics. Plant Physiology, 144: 1890–1898.

BRODRIBB, T. J., T. S. FEILD, AND L. SACK. 2010. Viewing leaf structure and evolution from a hydraulic perspective. Functional Plant Biology, 37: 488–498.

BRODRIBB, T. J., AND N.M. HOLBROOK. 2004. Stomatal protection against hydraulic failure: a comparison of coexisting ferns and angiosperms. New Phytologist, 162: 663–670.

BRODRIBB, T. J., N. M. HOLBROOK, M. A. ZWIENIECKI, AND B. PALMA. 2005. Leaf hydraulic capacity in ferns, conifers and angiosperms: impacts on photosynthetic maxima. New Phytologist, 165: 839–846.

BRODRIBB, T. J., AND S. A. M. MCADAM. 2011. Passive origins of stomatal control in vascular plants. Science, 331: 582–585.

BRONGNIART, A. 1828. Prodrome d'une histoire des végétaux fossiles. Grand dictionnaire d'Histoire Naturelle, paris, 57: 170–212.

CARLQUIST, S., AND E. L. SCHNEIDER. 2007. Tracheary elements in ferns: new techniques, observations, and concepts. American Fern Journal, 97: 199–211.

CHOAT, B., M. BALL, J. LULY, AND J. HOLTUM. 2003. Pit membrane porosity and water stress-induced cavitation in four co-existing dry rainforest tree species. Plant Physiology, 131: 41–48.

CHOAT, B., T. W. BRODIE, A. R. COBB, M. A. ZWIENIECKI, AND N. M. HOLBROOK. 2006. Direct measurements of intervessel pit membrane hydraulic resistance in two angiosperm tree species. American Journal of Botany, 93: 993–1000.

CHOAT, B., A. R. COBB, AND S. JANSEN. 2008. Structure and function of bordered pits: new discoveries and impacts on whole-plant hydraulic function. New Phytologist, 177: 608–626.

CHOAT, B., S. JANSEN, M. A. ZWIENIECKI, E. SMETS, AND N. M. HOLBROOK. 2004. Changes in pit membrane porosity due to deflection and stretching: the role of vestured pits. Journal of Experimental Botany, 55: 1569–1575.

CHOAT, B., AND J. PITTERMANN. 2009. New insights into bordered pit structure and cavitation resistance in angiosperms and conifers. New Phytologist, 182: 557–560.

CHRISTMAN, M. A., J. S. SPERRY, AND F. R. ADLER. 2009. Testing the 'rare pit' hypothesis for xylem cavitation resistance in three species of Acer. New Phytologist, 182: 664–674.

CHRISTMAN, M. A., J. S. SPERRY, AND D. D. SMITH. 2012. Rare pits, large vessels and extreme vulnerability to cavitation in a ring-porous tree species. New Phytologist, 193: 713–720.

CICHAN, M. A. 1985. Vascular cambium and wood development in Carboniferous plants. 2. *Sphenophyllum plurifoliatum* Williamson and Scott (Sphenophyllales). Botanical Gazette, 146: 395–403.

CICHAN, M. A. 1986a. Conductance in the wood of selected Carboniferous plants. Paleobiology, 12: 302–310.

CICHAN, M. A. 1986b. Vascular cambium and wood development in carboniferous plants. 3. *Arthropitys* (Equisetales, Calamitaceae). Canadian Journal of Botany-Revue Canadienne De Botanique, 64: 688–695.

CICHAN, M. A. 1986c. Vascular cambium and wood development in Carboniferous plants .4. Seed Plants. Botanical Gazette, 147: 227–235.

CICHAN, M. A., AND T. N. TAYLOR. 1982. Vascular cambium development in *Sphenophyllum*, Carboniferous arthrophyte. IAWA Bulletin, 3: 155–160.

CLEAL, C. J., J. P. LAVEINE, AND C. H. SHUTE. 1996. Architecture of the Upper Carboniferous pteridosperm frond *Macroneuropteris macrophylla*. Palaeontology, 39: 561–582.

CLEARWATER, M. J., AND C. J. CLARK. 2003. In vivo magnetic resonance imaging of xylem vessel contents in woody lianas. Plant, Cell & Environment, 26: 1205–1214.

CLEARWATER, M. J., AND G. GOLDSTEIN, 2005, Embolism repair and long distance water transport, p. 375–401. *In* N. M. Holbrook and M. A. Zweiniecki (eds.), Vascular Transport in Plants. Academic Press.

COCHARD, H., F. FROUX, F. F. S. MAYR, AND C. COUTAND. 2004. Xylem wall collapse in water-stressed pine needles. Plant Physiology, 134: 401–408.

COCHARD, H., T. HOELTTAE, S. HERBETTE, S. DELZON, AND M. MENCUCCINI. 2009. New insights into the mechanisms of water-stress-induced cavitation in conifers. Plant Physiology, 151: 949–954.

COMSTOCK, J. P., AND J. S. SPERRY. 2000. Theoretical considerations of optimal conduit length for water transport in vascular plants. New Phytologist, 148: 195–218.

CÔTE, W. A., 1967, Wood Ultrastructure: An Atlas Of Electron Micrographs. University of Washington Press.

DE BOER, H. J., M. B. EPPINGA, M. J. WASSEN, AND S. C. DEKKER. 2012. A critical transition in leaf evolution facilitated the Cretaceous angiosperm revolution. Nature Communications, 3: 1221.

DECOMBEIX, A.-L., B. MEYER-BERTHAUD, AND J. GALTIER. 2011a. Transitional changes in arborescent lignophytes at the Devonian–Carboniferous boundary. Journal of the Geological Society, 168: 547–557.

DECOMBEIX, A.-L., B. MEYER-BERTHAUD, J. GALTIER, J. A. TALENT, AND R. MAWSON. 2011b. Arborescent lignophytes in the Tournaisian vegetation of Queensland (Australia): Palaeoecological and palaeogeographical significance. Palaeogeography, Palaeoclimatology, Palaeoecology, 301: 39–55.

DECOMBEIX, A .L., B. MEYER-BERTHAUD, N. ROWE, AND J. GALTIER. 2005. Diversity of large woody lignophytes preceding the extinction of *Archaeopteris*: New data from the middle Tournaisian of Thuringia (Germany). Review of Palaeobotany and Palynology, 137: 69–82.

Delevoryas, T. 1955. The medullosae: structure and relationships. Palaeontographica B, 97: 114–167.

DELZON, S., C. DOUTHE, A. SALA, AND H. COCHARD. 2010. Mechanism of water-stress induced cavitation in conifers: bordered pit structure and function support the hypothesis of seal capillary-seeding. Plant Cell and Environment, 33: 2101–2111.

DIXON, H. H. 1914. Transpiration and the ascent of sap in plants. MacMillan and Co., London.

DIXON, H. H., AND J. JOLY. 1895. On the ascent of sap. Philosophical Transactions of the Royal Society B-Biological Sciences, 186: 563–576.

DOMEC, J.-C., B. LACHENBRUCH, AND F. C. MEINZER. 2006. Bordered pit structure and function determine spatial patterns of air-seeding thresholds in xylem of Douglas Fir (*Pseudotsuga menziesii*; Pinaceae) trees. American Journal of Botany, 93: 1588–1600.

DOMEC, J.-C., B. LACHENBRUCH, F. C. MEINZER, D. R. WOODRUFF, J. M. WARREN, AND K. A. MCCULLOH. 2008. Maximum height in a conifer is associated with conflicting requirements for xylem design. Proceedings of the National Academy of Sciences, 105: 12069–12074.

DOMEC, J.-C., J. M. WARREN, F. C. MEINZER, AND B. LACHENBRUCH. 2009. Safety factors for xylem failure by implosion and air-seeding within roots, trunks and branches of young and old conifer trees. IAWA Journal, 30: 101–120.

EDWARDS, D. 2003. Xylem in early tracheophytes. Plant Cell and Environment, 26: 57–72.

Feild, T. S., D. S. Chatelet, and T. J. Brodribb. 2009. Ancestral xerophobia: a hypothesis on the whole plant ecophysiology of early angiosperms. Geobiology, 7: 237–264.

FEILD, T. S., AND J. P. WILSON. 2012. Evolutionary voyage of angiosperm vessel structure-function and its significance for early angiosperm success. International Journal of Plant Sciences, 173: 596–609.

FISHER, J. B., H. T. W. TAN, AND L. P. L. TOH. 2002. Xylem of rattans: vessel dimensions in climbing palms. American Journal of Botany, 89: 196–202.

GALTIER, J. 1970. Recherches sur les vegetaux a structure conserve du Carbonifere inferieur francais. Paleobiologie Continentale, 1: 1–221.

GALTIER, J., AND B. MEYER-BERTHAUD. 2006. The diversification of early arborescent seed ferns. Journal of the Torrey Botanical Society, 133: 7–19.

GALTIER, J., B. MEYER-BERTHAUD, AND C. B. BECK. 1993. Large *Calamopitys* stems from the Tournaisian of France. Palaeontographica Abteilung B, 230: 59–79.

GIUDICE, G. E., M. L. LUNA, C. CARRION, AND E. R. DE LA SOTA. 2008. Revision of the genus *Salpichlaena* J. Sm. (Blechnaceae, Pteridophyta). American Fern Journal, 98: 49–60.

GLASSPOOL, I., J. HILTON, M. E. COLLINSON, AND W. SHI-JUN. 2004a. Defining the gigantopterid concept: a reinvestigation of *Gigantopteris* (*Megalopteris*) *nicotianaefolia* Schenck and its taxonomic implications. Palaeontology, 47: 1339–1361.

GLASSPOOL, I. J., J. HILTON, M.E. COLLINSON, S.-J. WANG, AND S. LI CHENG. 2004b. Foliar

physiognomy in Cathaysian gigantopterids and the potential to track Palaeozoic climates using an extinct plant group. Palaeogeography, Palaeoclimatology, Palaeoecology, 205: 69–110.

GRAHAM, L. E., AND J. GRAY. 2001, The origin, morphology, and ecophysiology of early embryophytes: neontological and paleontological perspectives, p. 140–159. *In* Gensel, P. G., and D. Edwards. (eds.), Plants Invade The Land: Evolutionary and Environmental Perspectives. Columbia University Press, New York.

HACKE, U. G., AND S. JANSEN. 2009. Embolism resistance of three boreal conifer species varies with pit structure. New Phytologist, 182: 675–686.

HACKE, U. G., AND J. S. SPERRY. 2001. Functional and ecological xylem anatomy. Perspectives IN PLANT ECOLOGY EVOLUTION AND SYSTEMATICS, 4: 97–115.

HACKE, U. G., J. S. SPERRY, T. S. FEILD, Y. SANO, E. H. SIKKEMA, AND J. PITTERMANN. 2007. Water transport in vesselless angiosperms: conducting efficiency and cavitation safety. International Journal of Plant Sciences, 168: 1113–1126.

HACKE, U. G., J. S. SPERRY, AND J. PITTERMANN. 2000. Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. Basic and Applied Ecology, 1: 31–41.

HACKE, U. G., J. S. SPERRY, AND J. PITTERMANN. 2004. Analysis of circular bordered pit function: II. Gymnosperm tracheids with torus-margo pit membranes. American Journal of Botany, 91: 386–400.

HACKE, U. G., J. S. SPERRY, W. T. POCKMAN, S. D. DAVIS, AND K. A. MCCULLOCH. 2001a. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia, 126: 457–461.

HACKE, U. G., J. S. SPERRY, J. K. WHEELER, AND L. CASTRO. 2006. Scaling of angiosperm xylem structure with safety and efficiency. Tree Physiology, 26: 689–701.

HACKE, U. G., V. STILLER, J. S. SPERRY, J. PITTERMANN, AND K. A. MCCULLOH. 2001b. Cavitation fatigue. Embolism and refilling cycles can weaken the cavitation resistance of xylem. Plant Physiology, 125: 779–786.

HARTMAN, C. M., AND H. P. BANKS. 1980. Pitting in *Psilophyton dawsonii*, an Early Devonian trimerophyte. American Journal of Botany, 67: 400–412.

HOLBROOK, N. M., E. T. AHRENS, M. J. BURNS, AND M. A. ZWIENIECKI. 2001. In vivo observation of cavitation and embolism repair using magnetic resonance imaging. Plant Physiology, 126: 27–31.

HURTT, G. C., J. FISK, R. Q. THOMAS, R. DUBAYAH, P. R. MOORCROFT, AND H. H. SHUGART. 2010. Linking models and data on vegetation structure. Journal of Geophysical Research-Biogeosciences, 115: G00E10.

ISE, T., AND P. R. MOORCROFT. 2010. Simulating boreal forest dynamics from perspectives of ecophysiology, resource availability, and climate change. Ecological Research, 25: 501–511.

JANSEN, S., B. CHOAT, AND A. PLETSERs. 2009. Morphological variation of intervessel pit membranes and implications to xylem function in angiosperms. American Journal of Botany, 96: 409–419.

JANSEN, S., Y. SANO, B. CHOAT, D. RABAEY, F. LENS, AND R. R. DUTE. 2007. Pit membranes in tracheary elements of Rosaceae and related families: new records of tori and pseudotori. American Journal of Botany, 94: 503–514.

JOHNSON, D. M., J.-C. DOMEC, D. R. WOODRUFF, K. A. MCCULLOH, AND F. C. MEINZER. 2013. Contrasting hydraulic strategies in two tropical lianas and their host trees. American Journal of Botany, 100: 374–383.

KOHN, M. J., AND M. H. THIEMENS. 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)ecology and (paleo)climate. Proceedings of the National Academy of Sciences of the United States of America, 107: 19691–19695.

LANCASHIRE, J. R., AND A. R. ENNOS. 2002. Modelling the hydrodynamic resistance of bordered pits. Journal of Experimental Botany, 53: 1485–1493.

LI, H., AND D. W. TAYLOr. 1998. *Aculeovinea yunguiensis* gen. et sp. nov. (Gigantopteridales), a new taxon of gigantopterid stem from the Upper Permian of Guizhou Province, China. International Journal of Plant Sciences, 159: 1023–1033.

LI, H., AND D. W. TAYLOR. 1999. Vessel-bearing stems of *Vasovinea tianii* gen. et sp. nov. (Gigantopteridales) from the Upper Permian of Guizhou Province, China. American Journal of Botany, 86: 1563–1575.

LI, H. Q., E. L. TAYLOR AND T. N. TAYLOR. 1996. Permian vessel elements. Science, 271: 188–189.

LUNA, M. L., G. E. GIUDICE, AND E. R. DE LA SOTA. 2008. Observations on tracheary elements in *Salpichlaena* J. Sm. (Blechnaceae, Pteridophyta). American Fern Journal, 98: 61–70.

McAdam, S. A. M., and T. J. Brodribb. 2012. Stomatal innovation and the rise of seed plants. Ecology Letters, 15: 1–8.

MEDVIGY, D., AND P. R. MOORCROFT. 2012. Predicting ecosystem dynamics at regional scales: an evaluation of a terrestrial biosphere model for the forests of northeastern North America. Philosophical Transactions of the Royal Society B-Biological Sciences, 367: 222–235.

MEDVIGY, D., S. C. WOFSY, J. W. MUNGER, D. Y. HOLLINGER, AND P. R. MOORCROFT. 2009. Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem

Demography model version 2. Journal of Geophysical Research-Biogeosciences, 114: G01002.

MEDVIGY, D., S. C. WOFSY, J. W. MUNGER, AND P. R. MOORCROFT. 2010. Responses of terrestrial ecosystems and carbon budgets to current and future environmental variability. Proceedings of the National Academy of Sciences of the United States of America, 107: 8275–8280.

MEYER-BERTHAUD, B., S. E. SCHECKLER, AND J.-L. BOUSQUET. 2000. The development of *Archaeopteris*: new evolutionary characters from the structural analysis of an Early Famennian trunk from southeast Morocco. American Journal of Botany, 87: 456–468.

MOORCROFT, P. R., G. C. HURTT, AND S. W. PACALA. 2001. A method for scaling vegetation dynamics: The ecosystem demography model (ED). Ecological Monographs, 71: 557–585.

NIKLAS, K. J. 1985. The evolution of tracheid diameter in early vascular plants and its implications on the hydraulic conductance of the primary xylem strand. Evolution, 39: 1110–1122.

NIKLAS, K. J. 1994. Morphological evolution through complex domains of fitness. Proceedings of the National Academy of Sciences of the United States of America, 91: 6772–6779.

NIKLAS, K. J. 1997. The Evolutionary Biology of Plants. University of Chicago Press, Chicago, IL, 470 p.

PHILIPPE, M., AND M. K. BAMFORD. 2008. A key to morphogenera used for Mesozoic conifer-like woods. Review of Palaeobotany and Palynology, 148: 184–207.

PHILIPPE, M., B. GOMEZ, V. GIRARD, C. COIFFARD, V. DAVIERO-GOMEZ, F. THEVENARD, J.-P. BILLON-BRUYAT, M. GUIOMAR, J.-L. LATIL, J. LE LOEUFF, D. NÉRAUDEAU, D. OLIVERO, AND J. SCHLÖGL. 2008. Woody or not woody? Evidence for early angiosperm habit from the Early Cretaceous fossil wood record of Europe. Palaeoworld, 17: 142–152.

PITTERMANN, J. 2010. The evolution of water transport in plants: an integrated approach. Geobiology, 8: 112–139.

PITTERMANN, J., B. CHOAT, S. JANSEN, S.A. STUART, L. LYNN, AND T. E. DAWSON. 2010. The relationships between xylem safety and hydraulic efficiency in the Cupressaceae: The evolution of pit membrane form and function. Plant Physiology, 153: 1919–1931.

PITTERMANN, J., AND J. SPERRY. 2003. Tracheid diameter is the key trait determining the extent of freezing-induced embolism in conifers. Tree Physiology, 23: 907–914.

PITTERMANN, J., AND J. S. SPERRY. 2006. Analysis of freeze-thaw embolism in conifers. The interaction between cavitation pressure and tracheid size.

Plant Physiology, 140: 374–382.

PITTERMANN, J., J. S. SPERRY, U. G. HACKE, J. K. WHEELER, AND E. H. SIKKEMA. 2005. Torus-margo pits help conifers compete with angiosperms. Science, 310: 1924–1924.

PITTERMANN, J., J. S. SPERRY, U. G. HACKE, J. K. WHEELER, AND E. H. SIKKEMA. 2006a. Inter-tracheid pitting and the hydraulic efficiency of conifer wood: the role of tracheid allometry and cavitation protection. American Journal of Botany, 93: 1265–1273.

PITTERMANN, J., J. S. SPERRY, J. K. WHEELER, U. G. HACKE, AND E. H. SIKKEMA. 2006b. Mechanical reinforcement of tracheids compromises the hydraulic efficiency of conifer xylem. Plant Cell and Environment, 29: 1618–1628.

POCKMAN, W. T., J. S. SPERRY, AND J. W. O'LEARY. 1995. Sustained and significant negative water-pressure in xylem. Nature, 378: 715–716.

RABAEY, D., F. LENS, E. SMETS, AND S. JANSEN. 2006. The micromorphology of pit membranes in tracheary elements of Ericales: new records of tori or pseudo-tori? Annals of Botany, 98: 943–951.

RAVEN, J. A., AND D. EDWARDS. 2001. Roots: evolutionary origins and biogeochemical significance. Journal of Experimental Botany, 52: 381–401.

ROWE, N., S. ISNARD, AND T. SPECK. 2004. Diversity of mechanical architectures in climbing plants: An evolutionary perspective. Journal of Plant Growth Regulation, 23: 108–128.

ROWE, N. P., AND J. GALTIER. 1988. A large calamopityacean stem compression yielding anatomy from the Lower Carboniferous of France. Geobios, 21: 109–115.

ROWE, N. P., T. SPECK, AND J. GALTIER. 1993. Biomechanical analysis of a paleozoic gymnosperm stem. Proceedings of the Royal Society of London Series B-Biological Sciences, 252: 19–28.

ROYER, D. L. 2006. CO_2-forced climate thresholds during the Phanerozoic. Geochimica Et Cosmochimica Acta, 70: 5665–5675.

SANO, Y., AND S. JANSEN. 2006. Perforated pit membranes in imperforate tracheary elements of some angiosperms. Annals of Botany, 97: 1045–1053.

SCHECKLER, S. E. 1978. Ontogeny of progymnosperms, 2. Shoots of Upper Devonian Archaeopteridales. Canadian Journal of Botany-Revue Canadienne De Botanique, 56: 3136–3170.

SECCHI, F., AND M. A. ZWIENIECKI. 2011. Sensing embolism in xylem vessels: the role of sucrose as a trigger for refilling. Plant, Cell & Environment, 34: 514–524.

SECCHI, F., AND M. A. ZWIENIECKI. 2012. Analysis of xylem sap from functional (nonembolized) and nonfunctional (embolized) vessels of *Populus*

nigra: chemistry of refilling. Plant Physiology, 160: 955–964.

SPECK, T., AND N. P. ROWE. 1994. Biomechanical analysis of *Pitus dayi*: early seed plant vegetative morphology and its implications on growth habit. Journal of Plant Research, 107: 443–460.

SPERRY, J. S. 1986. Relationship of xylem embolism to xylem pressure potential, stomatal closure, and shoot morphology in the palm *Rhapis excelsa*. Plant Physiology, 80: 110–116.

SPERRY, J. S. 2003. Evolution of water transport and xylem structure. International Journal of Plant Sciences, 164: S115–S127.

SPERRY, J. S., AND U. G. HACKE. 2004. Analysis of circular bordered pit function I. Angiosperm vessels with homogenous pit membranes. American Journal of Botany, 91: 369–385.

SPERRY, J. S., U. G. HACKE, T. S. FEILD, Y. SANO, AND E. H. SIKKEMA. 2007. Hydraulic consequences of vessel evolution in angiosperms. International Journal of Plant Sciences, 168: 1127–1139.

SPERRY, J. S., U. G. HACKE, R. OREN, AND J. P. COMSTOCK. 2002. Water deficits and hydraulic limits to leaf water supply. Plant Cell and Environment, 25: 251–263.

SPERRY, J. S., U. G. HACKE, AND J. PITTERMANN. 2006. Size and function in conifer tracheids and angiosperm vessels. American Journal of Botany, 93: 1490–1500.

SPERRY, J. S., U. G. HACKE, AND J. K. WHEELER. 2005. Comparative analysis of end wall resistivity in xylem conduits. Plant Cell and Environment, 28: 456–465.

SPERRY, J. S., F. C. MEINZER, AND K. A. MCCULLOH. 2008. Safety and efficiency conflicts in hydraulic architecture: scaling from tissues to trees. Plant, Cell & Environment, 31: 632–645.

SPERRY, J. S., K. L. NICHOLS, J. E. M. SULLIVAN, AND S. E. EASTLACK. 1994. Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. Ecology, 75: 1736–1752.

SPERRY, J. S., N. Z. SALIENDRA, W. T. POCKMAN, H. COCHARD, P. CRUIZIAT, S. D. DAVIS, F. W. EWERS, AND M. T. TYREE. 1996. New evidence for large negative xylem pressures and their measurement by the pressure chamber method. Plant Cell and Environment, 19: 427–436.

SPERRY, J. S., AND J. E. M. SULLIVAN. 1992. Xylem embolism in response to freeze-thaw cycles and water-stress in ring-porous, diffuse-porous, and conifer species. Plant Physiology, 100: 605–613.

SPERRY, J. S., AND M. T. TYREE. 1988. Mechanism of water stress-induced xylem embolism. Plant Physiology, 88: 581–587.

SPERRY, J. S., AND M. T. TYREE. 1990. Water-stress-induced xylem embolism in 3 species of conifers. Plant Cell and Environment, 13: 427–436.

STULL, G. W., W. A. DIMICHELE, H. J. FALCON-LANG, W. J. NELSON, AND S. ELRICK. 2012. Palaeoecology of *Macroneuropteris scheuchzeri*, and its implications for resolving the paradox of "xeromorphic" plants in Pennsylvanian wetlands. Palaeogeography, Palaeoclimatology, Palaeoecology, 331: 162–176.

TAIZ, L., AND E. ZEIGER. 2002. Plant Physiology. Sinauer Associates, Inc, Sunderland, MA, 690 p.

TAYLOR, T. N., E. L. TAYLOR, AND M. KRINGS. 2008. Paleobotany: The Biology and Evolution of Fossil Plants. Academic Press, Burlington, MA, 1230 p.

TOTZKE, C., T. MIRANDA, W. KONRAD, J. GOUT, N. KARDJILOV, M. DAWSON, I. MANKE, AND A. ROTH-NEBELSICK. 2013. Visualization of embolism formation in the xylem of liana stems using neutron radiography. Annals of Botany, 111: 723–730.

TYREE, M. T., AND F. W. EWERS. 1991. Tansley Review No. 34. The hydraulic architecture of trees and other woody plants. New Phytologist, 119: 345–360.

TYREE, M. T., AND J. S. SPERRY. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water-stress: answers from a model. Plant Physiology, 88: 574–580.

TYREE, M. T., AND J. S. SPERRY. 1989. Vulnerability of xylem to cavitation and embolism. Annual Review of Plant Physiology and Plant Molecular Biology, 40: 19–38.

TYREE, M. T., AND M. H. ZIMMERMANN. 2002. Xylem Structure and the Ascent of Sap. Springer-Verlag, Berlin, 283 p.

VAN DEN HONERT, T. H. 1948. Water transport in plants as a catenary process. Discussions of the Faraday Society, 3: 146–153.

VERES, J. S. 1990. Xylem anatomy and hydraulic conductance of Costa Rican Blechnum ferns. American Journal of Botany, 77: 1610–1625.

WAGNER, A., L. DONALDSON, H. KIM, L. PHILLIPS, H. FLINT, D. STEWARD, K. TORR, G. KOCH, U. SCHMITT, AND J. RALPH. 2009. Suppression of 4-coumarate-coa ligase in the coniferous gymnosperm *Pinus radiata*. Plant Physiology, 149: 370–383.

WHEELER, J. K., J. S. SPERRY, U. G. HACKE, AND N. HOANG. 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 and Environment, 28: 800–812.

WHEELER, T. D., AND A. D. STROOCK. 2008. The transpiration of water at negative pressures in a synthetic tree. Nature, 455: 208–212.

WILSON, J. P., AND W. W. FISCHER. 2011. Hydraulics of *Asteroxylon mackei*, an early Devonian vascular plant, and the early evolution of water transport

tissue in terrestrial plants. Geobiology, 9: 121–130.

WILSON, J. P., AND A. H. KNOLL. 2010. A physiologically explicit morphospace for tracheid-based water transport in modern and extinct seed plants. Paleobiology, 36: 335–355.

WILSON, J. P., A. H. KNOLL, N. M. HOLBROOK, AND C. R. MARSHALL. 2008. Modeling fluid flow in *Medullosa*, an anatomically unusual Carboniferous seed plant. Paleobiology, 34:472–493.

WNUK, C., AND H. W. PFEFFERKORN. 1984. The life habits and paleoecology of Middle Pennsylvanian medullosan pteridosperms based on an in situ assemblage from the Bernice Basin (Sullivan County, Pennsylvania, USA). Review of Palaeobotany and Palynology, 41:329–351.

ZIMMERMANN, M. H. 1983. Xylem Structure and the Ascent of Sap. Springer-Verlag, Berlin.

ZODROW, E. L. 2003. Foliar forms of *Macroneuropteris scheuchzeri* (Pennsylvanian, Sydney Coalfield, Nova Scotia, Canada). Atlantic Geology, 39:23–37.