

EVOLUTION OF WATER TRANSPORT AND XYLEM STRUCTURE

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Land plants need water to replace the evaporation that occurs while atmospheric CO₂ is diffusing into photosynthetic tissue. The water-for-carbon exchange rate is poor, and evolutionary history indicates a progression of innovations for cheap water transport—beginning in order with capillary suction at cell walls, stomatal regulation, hydroids, tracheids, secondary xylem, endodermis, and vessels. The radiation of plants in the Silurian and Devonian occurred when the need for water was at an all-time low because of high CO₂ concentration. Transport improvements appeared as water demand increased and CO₂ dropped to current values in the Carboniferous and Permian. Stomatal regulation and high-conductivity conduits permitted larger plants and a transition from poikilohydric to homiohydric water relations. The evolution of conduits from hydroids through tracheids to vessels reflects the need to balance resistance to implosion and cavitation versus maximum hydraulic conductance and minimum conduit investment. Localization of rigidifying lignin away from the lumen surface and porous wall regions during tracheid evolution, and the origin of pits, acted to maintain wall strength and permeability while minimizing cavitation. Vessels mark the pinnacle of efficiency, making vines and dense, stiff woods possible without sacrificing conductivity or cavitation resistance. However, vessels make cavitation-resistant wood more expensive and may compromise refilling efficiency versus tracheids. Vascular networks maximize hydraulic conductivity and protection from cavitation at minimum investment by following Murray's law and localizing resistances to the periphery. A future challenge is to quantify the significance of xylem structure in terms of the carbon cost of transpiration and the net carbon profit via gas exchange.

Keywords: xylem evolution, ecological wood anatomy, cavitation, plant water relations.

The photosynthetic tissues of terrestrial plants require a water supply to avoid drying out while atmospheric CO₂ is diffusing to the chloroplasts. The adaptive radiation of plant growth form and habitat has necessarily been accompanied by the evolution of specialized water supply systems. This overview focuses on requirements of land plant water transport in an evolutionary context.

The Need for Water Transport

The plant's need for water parallels the amount of transpiration during gas exchange; other water requirements for growth and photosynthesis pale in comparison. The maximum gradient for plant water loss to the atmosphere (D) has remained constant during plant evolution (maximum D = saturated vapor pressure, e.g., 2.3 kPa at 20°C). In contrast, the maximum available gradient for CO₂ diffusion (= atmospheric partial pressure) has fluctuated widely from a high of ca. 0.5 kPa (ca. 5000 ppm) at the origin of land plants down to ca. 0.03 kPa during late Carboniferous and again during preindustrial times (fig. 1; Berner and Kothavala 2001). The water use efficiency (WUE) for terrestrial photosynthesis will have fluctuated accordingly—over a 17-fold range assuming constant ratios of leaf : atmosphere CO₂ partial pressure (P_i/P_a)

and diffusive conductance of water : CO₂ (g_h/g_c). So, while a Silurian C₃ plant at the highest CO₂ concentration would lose only 22 molecules of water per molecule of CO₂ at $D = 1.5$ kPa, a late Carboniferous plant would have to lose 390 water molecules ($P_i/P_a = 0.8$, $g_h/g_c = 1.6$; fig. 1). Although plants can control their WUE to some extent by adjustments in leaf temperature and photosynthetic capacity (Lambers et al. 1998), the physiological range of WUE will be dictated by atmospheric CO₂ concentration.

The colonization of land and origin of most major clades by the early Carboniferous (fig. 1, bottom) was probably facilitated by very high atmospheric CO₂ concentration at the time. For the same net carbon gain and water-potential regime, a Silurian plant would require a hydraulic conductance (transpiration rate per water-potential drop) on the order of 17 times lower per unit transpiring area than a late Carboniferous one. Similarly, a given internal storage capacity (= capacitance) would supply transpired water for 17 times longer under Silurian compared to late Carboniferous conditions. High CO₂ conditions would have favored relatively low hydraulic conductance systems with high capacitance—a fortuitous combination for the origin of nonvascular and early vascular plants with necessarily limited transport capacities and inherently good capacitance because of the thin and elastic cell walls of parenchyma tissue.

However, even in the best of times, the demand for water was high relative to CO₂ supply. The evolving water-transport system had to be energetically efficient to avoid starving the

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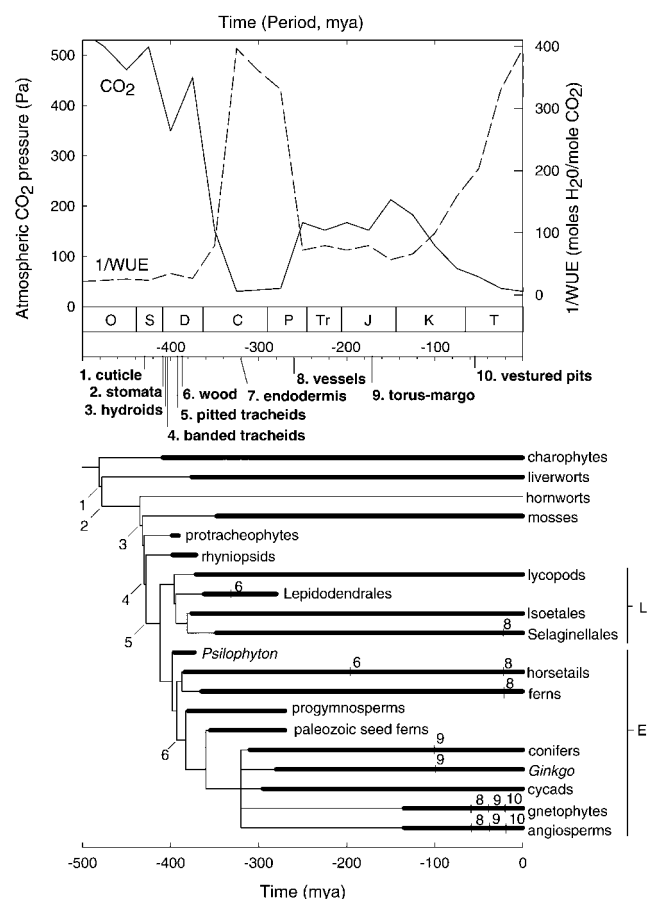


Fig. 1 Events in land plant history versus geologic period and millions of years ago (mya). Graph (top) shows atmospheric CO₂ concentration (solid line; Berner and Kothavala 2001) and moles of water transpired per moles of CO₂ fixed (inverse of water use efficiency, 1/WUE, dashed line) at a vapor pressure deficit of 1.5 and a ratio of leaf : atmospheric CO₂ partial pressure of 0.8. Time line on lower axis shows earliest appearance of features in the fossil record (wood = secondary xylem). Phylogeny at bottom (Kenrick and Crane 1997b; from Doyle 1998; Judd et al. 2002) shows hypothetical relationships among extant and selected fossil plants. Heavy lines indicate presence in fossil record. Vertical bars at right indicate the lycophyte (L) and euphyllophyte (E) clades of vascular plants. The seemingly rapid appearance of many land plant features in the late Silurian is in part an artifact of the lack of appropriate terrestrial sediments during this time (Kenrick and Crane 1997a). Placement of numbered features (corresponding to fossil time line) on the phylogeny, timing of divergence, and fossil data from Beck et al. 1982; Kenrick and Crane 1991; Stewart and Rothwell 1993; Carlquist 1994; Li et al. 1996; Kenrick and Crane 1997a, 1997b; Doyle 1998; Ligrone et al. 2000; Wellman and Gray 2000; Jansen et al. 2001; Raven and Edwards 2001. The endodermis (7) is not placed on the phylogeny because of ambiguous distribution and homology, particularly in fossil taxa where it can be difficult to detect (Raven and Edwards 2001).

plant. It is difficult to imagine a cheaper process for driving the transpiration stream than the cohesion-tension mechanism at work in vascular plants. The driving force comes free of charge courtesy of the automatic coupling between evaporation and negative pressure achieved by capillary forces in the

cell walls. Vascular investment is minimized by having water flow through high-conductance tubes of dead cells with minimal maintenance cost. The cost of transpiration is reduced to side effects of flow-induced negative apoplast pressure (“dynamic water stress”), the construction of the conduit network, and the few layers of living tissue between conduits and soil that filter the water.

In all probability, the evolution of the cohesion-tension mechanism was inevitable and straightforward. The basic ingredients would have been present in the most unspecialized green algal descendent to become stranded on land. All that is needed was a hydrophilic cell wall that can act as a wick for water movement, and this would have been inherited from the green algae that already have a high-tensile-strength wall of cellulose for osmoregulation.

Origin of Water-Conducting Tissue

In the absence of high-conductivity transport tissue, capillary suction will generate severe dynamic water stress. A pressure drop of 90 MPa m⁻¹ accompanies a modest transpiration rate of 5 mmol s⁻¹ m⁻² across parenchyma tissue typical of nonvascular plants (tissue conductivity = 5.5 × 10⁻¹¹ mol s⁻¹ Pa⁻¹ m⁻¹; Raven 1984). While this will not seriously stress the thin thallus of a liverwort, any path length over 2 cm will generate significantly low water potentials (below -2 MPa) at the downstream end. The first land plants, by analogy with their closest living nonvascular relatives, probably avoided excessive dynamic water stress by being small to reduce the pressure drop and having a cuticle (with or without air pores) on their photosynthetic surfaces to keep transpiration from exceeding their limited transport capacity. Along with spores, cuticle remnants are among the earliest fossil evidence of land plants (fig. 1).

These early land plants were necessarily “poikilohydric,” equilibrating their water potential with that of highly local water sources (Raven 1987) and depending on water-storage capacitance to extend their period of hydration. The desiccation tolerance so common in modern bryophytes and terrestrial green algae is undoubtedly an ancestral trait essential for survival on land in the absence of a specialized water-supply system (Oliver 1996).

The inevitability of capillary suction in nonvascular plants leads in a few conceptual steps to vascular plants with water conduction in dead cell wall skeletons. Dead water conduits efficiently couple the suction generation of an air-water meniscus in the nanoscale pores of the cell wall with the high hydraulic conductivity of the much wider lumen of the water-filled cell. A low-end xylem conductivity per area is 4 × 10⁻⁵ mol s⁻¹ Pa⁻¹ m⁻¹ (fig. 2), fully six orders of magnitude greater than the parenchyma-based water conduction of nonvascular plants. Higher conductivity per unit area provides four advantages: (1) less tissue investment in water transport, particularly because the dead conduits require no maintenance; (2) the potential for longer path length and larger plants; (3) less dynamic water stress; (4) potentially higher CO₂ diffusion rates—because higher rates of transpiration can be tolerated without excessive stress.

At a minimum, the only specializations required for development of a cell-skeleton conduit is the programmed death of

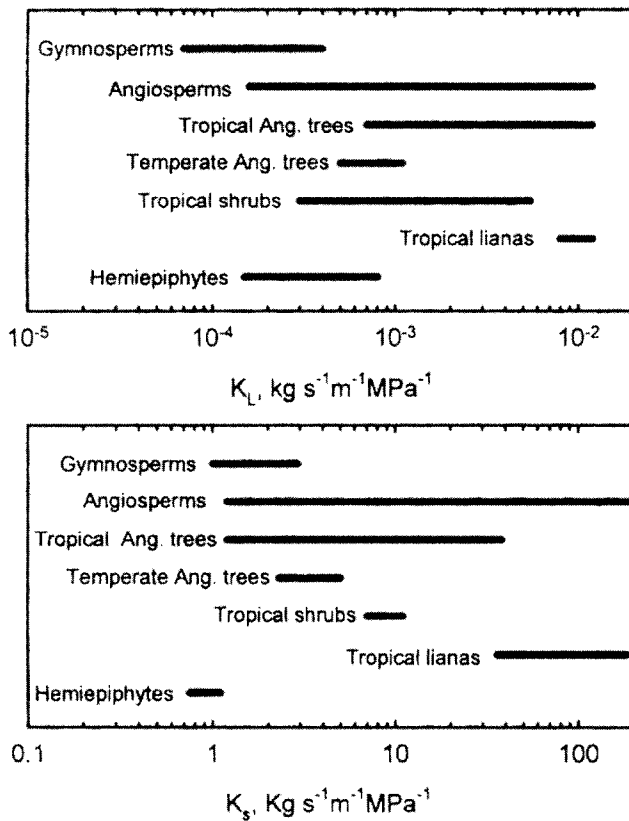


Fig. 2 Comparison of leaf-specific (K_L , top) and wood-specific (K_S , bottom) hydraulic conductivities in various wood types (to convert to text units of moles per second per pascal per meter, multiply conductivity values by 5.56×10^{-5} , from Tyree and Zimmermann 2002).

the protoplast and a compression-resistant cell wall to avoid collapse by negative pressure. These innovations were accomplished early, with unequivocal water-conducting cells present in the fossil record by 410 million years ago (mya; fig. 1). A wide range of conduit morphology was present by 390 mya (fig. 3).

The simplest conduits were thin and smooth-walled microperforate tubes of the now extinct protracheophytes (fig. 3A; *Aglaophyton*, *Horneophyton*; Kenrick and Crane 1991). These resemble the hydroids of some mosses and may have a common ancestry (fig. 1; Mishler and Churchill 1984; Kenrick and Crane 1997a; but Ligrone et al. 2000). These fossil tubes do not appear to have been lignified but may have been impregnated with lignin-like polyphenols, as are extant hydroids. Modern hydroids have limited rigidity, as evidenced by their tendency to collapse (Ligrone et al. 2000). While this would limit the pressure for water transport, it may allow extension in growing tissue, since hydroids otherwise lack the banded thickenings that permit longitudinal extension of protoxylem tracheary elements.

True tracheids have been defined as single-celled conduits with lignified and ornamented walls, either banded or pitted (Kenrick and Crane 1997a; Doyle 1998). They may have evolved once, uniting all tracheophytes (fig. 1, all taxa below the protracheophytes). The banded type (fig. 3B, 3C) super-

ficially resembles the modern protoxylem tracheid. It is thought to be ancestral because it is the only type found in the basal tracheophyte group, the extinct rhyniopsids. The additional presence of pitted elements (fig. 3D) resembling metaxylem characterizes most other tracheophyte groups (Kenrick and Crane 1991).

The lignified secondary walls of tracheary elements provide a significant increase in the compressive strength of the wall—from negligible in nonlignified walls to over 40 MPa (Niklas 1992). The negative pressure required to implode a tubular conduit is a function of the wall thickness divided by the conduit lumen diameter (fig. 4A), the specific equation depending on what type of stress (e.g., hoop vs. bending) induces failure (Young 1989). Assuming implosion by failure of the double wall dividing an air-filled from a water-filled conduit, a conduit with an equivalent circle diameter of 20 μm in diameter and lignified wall thickness of 2 μm can withstand ca. -3 MPa before imploding (fig. 4B, dashed line). Apparently, cavitation occurs before implosion pressures are reached, based on the rarity of tracheary element collapse. Estimated minimum safety factors from implosion (implosion/cavitation

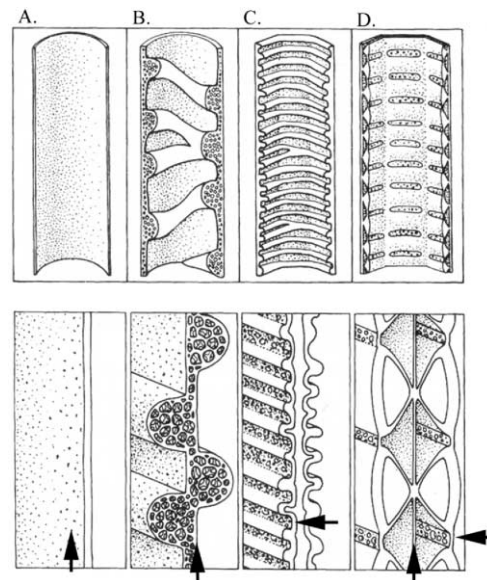


Fig. 3 Range of water conduit morphology in early fossil plants (top), with details of interconduit wall structure (below). Cells are ca. 20–40 μm in diameter. A, “Hydroid” type of conduit typical of some mosses (Ligrone et al. 2000) but also resembling that of extinct protracheophytes. Micropores (arrow) are derived from plasmodesmata. B, Banded thickenings of an “S”-type tracheid of a rhyniopsid. Micropores evenly distributed as in A, but the wall is two layered and ornamented. A decay-resistant and presumably lignified layer (arrow) faces the lumen and covers a spongy, possibly less lignified layer (Friedman and Cook 2000). C, Banded thickenings of a “G”-type tracheid of a basal extinct tracheophyte. Larger pores are present that are limited to thin areas of the wall (arrow). Wall is two layered as in B. D, Scalariform-pitted tracheid of an extinct *Psilophyton* species. Pit chamber and membrane (vertical arrow) is present. Thickened wall remains two layered, with lignified layer facing the lumen. Pit aperture consists of perforations in this layer (horizontal arrow). From fig. 5 of Kenrick and Crane (1997b).

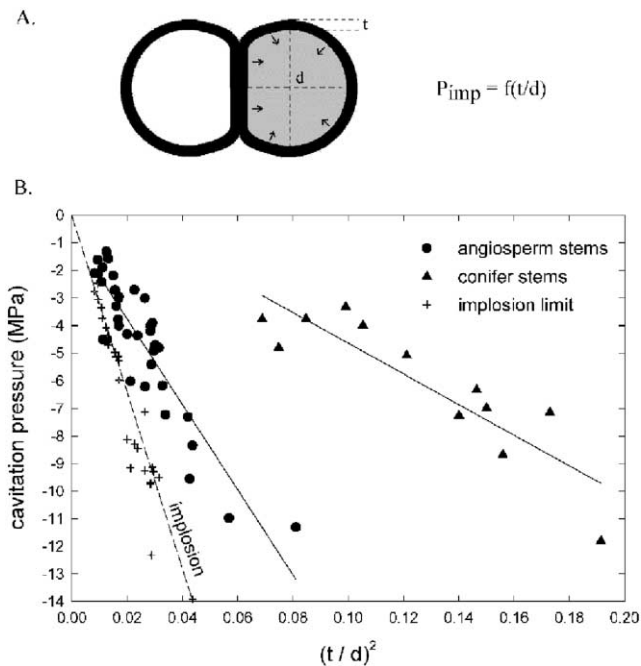


Fig. 4 A, Transverse section of two adjacent conduits, one air filled and one water filled (gray). Negative pressure pulls in on the wall of the water-filled conduit. The implosion pressure (P_{imp}) is a function of the ratio of the wall thickness (t) and lumen diameter (d). B, Cavitation pressure versus $(t/d)^2$ of angiosperm stem vessels (circles) and conifer stem tracheids (triangles). The P_{imp} is predicted to be proportional to $(t/d)^2$ for implosion by bending of interconduit walls (Young 1989). Wall dimensions of both conduit types scale with cavitation pressure to maintain a constant safety factor from implosion (dashed line). The average safety factor is larger in conifer stem tracheids (6.8) than in vessels (1.7). From Hacke et al. (2001a).

pressure) range from 1.7 in angiosperm vessels to 6.8 in conifer tracheids (fig. 4B). The higher number for conifers may relate to the additional role of their tracheids in supporting the tree (Hacke et al. 2001a).

Propping open tracheary elements was probably the original function of lignin and secondary walls in plants (Raven 1987). The thickened and presumably lignified walls of early Devonian vascular plants are limited to tracheary elements of a protostele—a cylindrical strand in the stem center. This position does not indicate a role in mechanical support because compressive forces from stem bending are greatest at the epidermis. These plants were small and capable of being supported hydrostatically (Vincent and Jeronimidis 1991; Niklas 1994). Nor would a central strand of lignified tissue be a direct barrier to herbivory, although lignin components may have evolved previously as a chemical defense (Raven 1987).

Lignin rigidifies the cell wall in part by replacing water in the cell wall matrix and pore space (Donaldson 2001). In so doing, it reduces the permeability of the walls to water—both by reducing wall porosity and because lignin is hydrophobic. This water-proofing action is not necessary to prevent leakage of water from the conduits as long as the water is under negative pressure, and it has the disadvantage of increasing resistance to water and solute flow across the conduit walls. Plas-

modesmat pores and especially pits provide passage, and their distribution in the low-permeability lignified walls provides control over where the movement of water and solutes can occur between vascular and nonvascular tissues. Conduit pitting may have evolved from the aggregation of plasmodesmata in response to greater need for interconduit permeability and transport between conduits and surrounding parenchyma (Edwards and Axe 2000).

Stomata

Without some means of regulating transpiration, plant water loss is at the mercy of D , passively tracking it regardless of consequences. The advantage of stomata is maintaining transpiration near its optimum (Cowan 1977). Too low a transpiration rate limits CO_2 uptake. Too high a transpiration saturates CO_2 uptake. More disastrously, an excessive transpiration rate leads to crippling effects of dynamic water stress, particularly as source water becomes less available. Problems include symplastic shrinkage and loss of turgor or costly production of organic compatible solutes (Morgan 1984). Direct inhibition of photosynthesis occurs at low symplast water potentials, reducing WUE (Kaiser 1987). Low apoplast pressure can reduce hydraulic conductivity—by cavitation in xylem conduits, drying of soil around absorbing organs, and by tissue and cell-wall shrinkage in nonvascular tissue. Loss of hydraulic conductivity leads to even greater negative pressures in a vicious cycle. Unless transpiration is slowed, this runaway loss of conductivity will desiccate the tissue before the source water is used up (Tyree and Sperry 1988; Sperry et al. 1998). A cuticle by itself can only reduce the range of transpiration rates, keeping the maximum rate at high D below a nonoptimal extreme. Only stomatal regulation can optimize transpiration under all conditions.

Water-conducting tissue and stomatal regulation go hand in hand. They appear at essentially the same time in the fossil record and co-occur in the vast majority of extant plants (fig. 1). The two features must be synergistic—providing the greatest benefit in coordination. Transport tissue minimizes dynamic water stress and permits larger plant size but cannot optimize transpiration rate and avoid uncontrolled loss of hydraulic conductivity. Stomatal regulation can protect tissue conductivity and optimize transpiration rate under variable environmental conditions, but this optimal rate will be impossibly small in nonvascular plants with a flow path greater than a few centimeters (Raven 1987).

Stomata may have evolved once—before water-conducting tissue in the lineage leading to the tracheophytes (fig. 1; Kenrick and Crane 1997a; Doyle 1998). Thus, hornworts have stomata but lack conducting cells. The opposite situation occurs in the dead-end liverwort line where water-conducting cells have arisen independently of moss hydroids and tracheids but stomata are absent (Ligrone et al. 2000). Stomata without conducting tissue could be advantageous in allowing slight increases in plant size or growth rate through the optimization of transpiration, but any benefit would have to subtract the added cost of stomatal regulation and may not pay in plants that are already small enough to avoid significant dynamic stress and possess desiccation tolerance. This is consistent with the absence of stomata in all liverworts and the apparent loss

of stomatal function or structure in many other bryophytes where they are found only on the sporophyte, which is “parasitic” on the gametophyte (Kenrick and Crane 1997a). Conversely, stomatal control would be less necessary in vascularized plants living in environments of relatively constant D and soil moisture where transpiration and water stress do not fluctuate widely. Higher plants grown under such conditions can lose their ability to regulate transpiration (Schulte and Hinckley 1987).

The Endodermis and Root Pressure

Just as nearly all vascular plants have stomata, nearly all have an endodermis with a waterproofing casparian strip of lignin and suberin (Schreiber 1996; Raven and Edwards 2001), whether or not the absorbing organs are true roots or are limited to stems. An interesting exception is *Lycopodium*, where an endodermis is lacking in roots but present in stems; however, an “endodermoid layer” in the roots seems to have the equivalent function (Raven 1984). The earliest appearance of an endodermis in the fossil record is from the Carboniferous (Raven 1984), but it likely originated at least as early as the split of the tracheophytes into the lycophyte and euphyllophyte clades (fig. 1).

The selective filter of an endodermis or equivalent layer of living tissue is probably essential for regulating the ionic composition of xylem sap and excluding pathogens and their toxins and other contaminants from the transpiration stream. The endodermis provides the additional capability of promoting osmotic “root pressures” that can push sap up the xylem and out of any hydathodes or other positive pressure leaks in the shoot when transpiration is minimal and soil moisture is high (Steudle et al. 1993). Many seedless vascular plants have an endodermis around the xylem of aerial shoots, perhaps to minimize outward leaks of pressure-driven sap into the air spaces of the photosynthetic tissue (Zimmermann 1983). Root pressures are known to refill cavitated conduits (Milburn and McLaughlin 1974; Sperry et al. 1987; Sperry and Sullivan 1992; Hacke and Sauter 1996). Like extant seedless plants, the earliest vascular plants lacked secondary growth. The inability to replace cavitated conduits by growth may have made the refilling power of root pressure an important corollary of evolving vascular tissue.

Consequences of Vascular Tissue and Stomatal Regulation

Both of these traits permit a larger plant size. In terms of water balance, larger size creates the potential for tapping a more stable water source via a subterranean absorbing system of rhizoids, stems, and ultimately roots (Raven and Edwards 2001). The result is a transition from poikilohydric to homiohydric water relations where plant water stress is regulated within a limited range compared to the dryness of air and soil surface (Raven 1987). In addition to enabling homiohydry, larger size of course permitted taller shoots for escaping shading by neighboring plants and improving long-distance aerial dispersal, leading to more diverse and complex shoot architectures.

The evolution of homiohydry was associated with the loss

of desiccation tolerance at the cellular level in vegetative cells, although this ancestral trait is retained in seeds, pollen, and spores of many vascular plants (Oliver 1996). The few vascular plants with vegetative desiccation tolerance tend to be less than a meter in height (Gaff 1981). The cost of desiccation tolerance would be unnecessary in truly homiohydric plants, perhaps leading to its disappearance. It is also probably impossible for vascular tissue to be desiccation tolerant in large plants. Reversing xylem cavitation requires pressures within a few kilopascals of atmospheric pressure for extended time periods (Yang and Tyree 1992). In taller plants, this would require root pressure or other active means of elevating xylem pressure, processes that may be limited in the rehydrating root tissue (Sherwin et al. 1998). In addition, the cell and tissue specialization for mechanical and transport needs of large plants may be incompatible with enduring the changes in symplast volume, disruption of plasmodesmatal connections, and cytoplasmic organization required of desiccation tolerance (Oliver 1996).

Origin of Basic Structure-Function Relationships in Xylem

Mechanical Considerations

Exploiting greater plant size required a shift from hydrostatic support of stems to support by lignified and thickened cell walls (Niklas 1990, 1994). The transition from hydrostatic support to cell-wall support of primary growth was probably first achieved by the evolution of sclerenchyma tissue located peripherally in the stem (Raven 1987; Speck and Vogellehner 1988). Even in the arborescent lycopsids with secondary xylem (e.g., *Lepidodendrales*; fig. 1), the wood was of limited extent near the stem center, and mechanical support was provided by an expanded cortex and periderm (Gifford and Foster 1989; Kenrick and Crane 1997a).

At first glance, having a peripheral support tissue system in addition to compressively strong vascular tissue seems wasteful duplication. However, the central location of the vascular tissue in the first vascular plants may have been necessary to protect it from bending stresses that could disrupt water transport by inducing collapse or cavitation. In more complex stelar patterns where the vascular tissue is dispersed throughout the axis, the tracheary elements are generally embedded in non-conducting sclerenchyma fibers as if to buffer the conduits from mechanical stress (Vincent and Jeronimidis 1991). This pattern extends to angiosperm vessels embedded in supporting fibers (fig. 6B).

The mechanical vulnerability of tracheary elements identifies a basic trade-off in their function; the wall strength required to counteract negative pressure and any additional bending stress from supporting the plant is likely to reduce permeability to water. The combination of support and transport in tracheids of “normal” secondary xylem ancestral to progymnosperms and seed plants (fig. 1) represents a derived condition that must minimize this trade-off, perhaps via the evolution of more sophisticated interconduit pitting that minimized the loss of mechanical strength for a given permeability to water (Beck et al. 1982).

Minimizing Cavitation

Lignified and thickened walls make large negative pressures possible in theory, but to achieve them cavitation must be prevented. The most basic requirement is to exclude air bubbles that can nucleate cavitation (Oertli 1971). Air bubbles are unlikely in newly produced conduits given their development from a dying water-filled cell. Air can be sucked through pores in the conduit wall to seed cavitation (Zimmermann 1983), but given the naturally small pore spaces in cell walls this is not a major difficulty. The air-seeding pressure of nanometer-scale pores in lignified cell walls (1.2–3.3 nm; Berlyn et al. 1995) is in excess of 15 MPa, even considering that hydrophobic lignin could significantly reduce the capillary force of the air-water meniscus by lowering its contact angle with the pore wall (Oertli 1971). However, a highly lignified and hydrophobic lumen surface could potentially trigger cavitation directly at the water-wall interface (Pickard 1981).

Tracheary elements from early fossil vascular plants and their closest living relatives appear to have the highest concentration of lignin adjacent to the cell lumen (fig. 3; Friedman and Cook 2000), seemingly maximizing the likelihood of cavitation at a hydrophobic interface. This situation is reversed in tracheary elements of higher plants, where lignin concentration is highest at the middle lamella, dropping to much lower values at the lumen (Panshin and de Zeeuw 1970; Donaldson 2001). Whether lignin can destabilize xylem water under negative pressure is unknown, but if so, the pattern of lignification could have important functional implications.

Cavitation can also occur from bubbles formed during freeze-thaw cycles (Hammel 1967). Conduits over 44 μm diameter limit are predicted to cavitate by freezing for a xylem pressure of -0.5 MPa (Davis et al. 1999). This applies regardless of the length of the conduit; tracheids and vessels have the same diameter constraint (Pittermann and Sperry 2003).

Minimizing Leaks

Leaks in the transpiration stream mean air entry, not sap exit. Damage to conduits opens up large holes and occurs in the course of extension growth by protoxylem rupture. An air-water interface across even a narrow conduit lumen of 10 μm diameter cannot withstand more than 30 kPa of suction before air enters (Zimmermann 1983). A secondary defense against such leaks is essential. Therein lies the necessity for the multiple-conduit transport network of plants as opposed to a single-conduit system such as in the mammalian cardiovascular system.

Interconduit Pitting

Interconduit pits are the check valves that permit water flow between conduits but inhibit the leaking of air into the transpiration stream (Dixon 1914). There are obvious trade-offs in their functioning because creating areas in the wall that are permeable to water flow will also weaken the strength of the wall and increase its vulnerability to air entry. Cavitation has been linked to air seeding at interconduit pits (Crombie et al. 1985; Cochard et al. 1992; Jarbeau et al. 1995; Sperry et al. 1996), meaning they are the weak link in the protection of the conduit network against air entry. Even so, pits significantly

increase the resistance to flow through the xylem—by as much as 30% or more (Schulte and Gibson 1988; Lancashire and Ennos 2002).

The pit membrane in extant plants is homologous with the nonlignified primary wall region between banded thickenings of protoxylem (Mauseth 1988). In an ontogeny-recapitulates-phylogeny argument, Kenrick and Crane (1997a) suggest that pitted metaxylem tracheids (fig. 3D) evolved from banded “protoxylem-type” tracheids that are exclusively present in rhyniopsids (fig. 1; fig. 3B, 3C), with the ancestral form persisting as protoxylem.

The structure of interconduit pits presumably represents an optimal compromise between maintaining strength and resistance to air entry of the interconduit wall without unduly sacrificing hydraulic conductivity of the pit (fig. 5A; Carlquist 1988). This excellent, but never evaluated, hypothesis presumably explains the functional significance of the great variety of pit shape, size, membrane structure, border configuration, ves-ture presence, and pit-field pattern in vascular plants.

The early stages of pit evolution seem conservative in favoring resistance to air entry and strength over conductivity to water (fig. 3). No pits are present in the hydroid type of conduit (fig. 3A). Water must move through uniformly distributed micropores of ca. 100 nm in diameter that are derived from plasmodesmata. The air-seeding pressure through such pores would be about 3 MPa, assuming a hydrophilic wall surface (Pickard 1981). The compressively stronger-banded tracheids (fig. 3B, 3C) still retain the decay-resistant (=lignified) layer (Kenrick and Crane 1991; Friedman and Cook 2000) between bands that would limit both permeability and also extensibility by comparison with extant protoxylem. Moreover, the presence of hydrophobic lignin in the porous regions could have seriously reduced capillary forces and air-seeding pressures by reducing the adhesion of water to the pore wall. The “G”-type banded tracheid (fig. 3C) seems an improvement over the “S” type (fig. 3B) because of the localization of larger pores (ca. 1500 nm diameter; Kenrick and Crane 1991) over the thin areas and the alignment of these zones between adjacent tracheids.

Early pitted tracheids (fig. 3D) have bordered scalariform pits that begin to resemble modern pitted tracheids. Importantly, the well-defined pit membrane appears nonlignified (and hence hydrophilic), which would maximize the air-seeding pressure for a given permeability. Circular bordered pits with homogeneously thin pit membranes (i.e., no torus) appear in progymnosperms of the late Devonian (Beck et al. 1982).

The way these early pits functioned was probably identical to the capillary-sealing action of most extant pits (fig. 5B). Uniformly small membrane pores, though possessing low hydraulic conductivity, are nonlignified and provide an effective capillary barrier to air entry. The air-seeding pressure of these pores can be enough to deflect the membrane to the pit border when one is present (fig. 5B; Thomas 1972). The border functions to support both the wall and the membrane against the bending force between an air-filled compared with water-filled conduit. Small or absent borders probably indicates weak and cavitation-prone conduits but high conductivity. Whether air seeding occurs by irreversible plastic yielding of the membrane (“creep”) or through reversible elastic stretching is unknown. Membrane creep may cause “cavitation fatigue,” where cav-

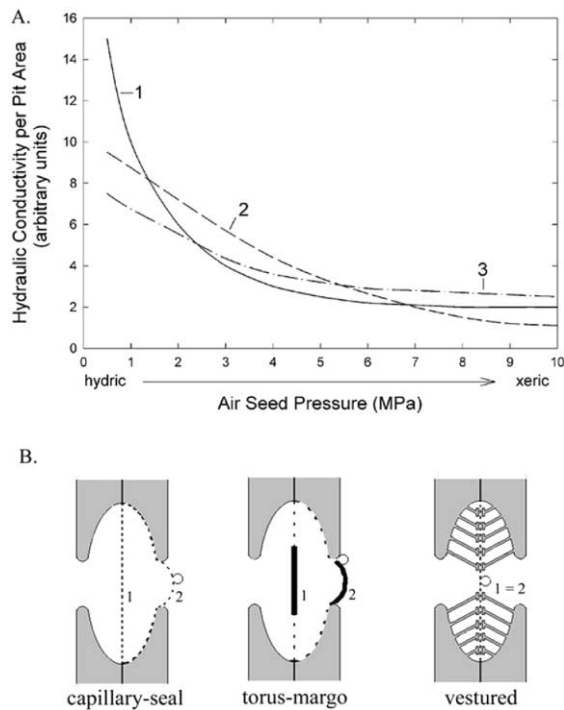


Fig. 5 A, Trade-off between the hydraulic conductivity of a pit versus its air-seeding pressure. The higher the air-seed pressure, the more xeric the habitat. Pits vulnerable to air seeding will have higher conductivity per pit area than pits resistant to air seeding because the structure needed to prevent air entry will also decrease conductivity to water flow. No single pit type is likely to have a superior conductivity over the entire air-seed range. For example, one pit type may be optimal for low air-seed pressures (e.g., 1), a second at intermediate pressures (e.g., 2), and a third at higher pressures (3). B, Three types of valve action in interconduit pits. Shaded area is the pit border formed by the lignified secondary wall. The nonlignified pit membrane spans the pit chamber, which opens to each conduit lumen through an aperture. Position 1 shows the membrane during water conduction when conduits on either side are water filled. Position 2 shows the membrane acting to prevent air entry from the left-hand conduit to a water-filled conduit on the right. The bubble at the membrane indicates air seeding of cavitation. Capillary sealing pits minimize air entry by having narrow pores in their pit membranes with high air-seeding pressure (Crombie et al. 1985; Sperry and Tyree 1988). Membranes probably aspirate prior to air seeding, and membranes are distorted. Torus-margo pits have a central thickened torus (thick bar in membrane) surrounded by a very porous margo. The air seal is formed by the aspiration of the torus over the pit aperture. Air seeding probably occurs when the torus edge is pulled through the aperture (Sperry and Tyree 1990). Vestured pits support the membrane by lignified struts from the pit chamber wall. There is no distortion of the membrane prior to air seeding, which occurs through membrane pores (Zweypfennig 1978).

itation renders a conduit more susceptible to subsequent cavitation (Hacke et al. 2001b).

Variations on the ancestral mode of pit function presumably evolved to maximize the pit hydraulic conductivity for a given air-seeding pressure and wall strength (fig. 5A). Circular bordered pits with a torus-margo configuration appear definitively in Jurassic conifers (fig. 1; Beck et al. 1982). Sealing requires

the aspiration of torus against the pit aperture. The aspiration is driven by capillary forces at the margo pores. Ultimately, air seeding occurs when the torus edge is pulled through the pit aperture (fig. 5B; Sperry and Tyree 1990). Although much of the membrane is taken up by the nonconducting torus, the surrounding margo can have relatively large pores. Given that conductance through short circular pores scales with their diameter to the third power (Vogel 1994), a margo with fewer large pores could have equal or greater total conductivity than a capillary sealing pit with more small pores. Larger margo pores do not directly compromise air seeding, which is prevented by the aspirated torus. A greater pit conductivity per air-seed pressure may explain the persistence of torus-margo pits in many extant conifers, *Ginkgo*, and *Ephedra* (Bauch et al. 1972) and its convergent evolution in certain angiosperms (Wheeler 1983; Dute 1987; Dute et al. 1990, 1996). This putative advantage of torus-margo pits would not necessarily apply to the full range of air-seed pressures.

A potential disadvantage of the torus-margo pit is that it may not be as reusable as capillary-sealing pits. Air drying of softwoods causes irreversible pit aspiration—a bane to preservative infusion in the timber industry. A permanently aspirated torus blocks water flow even if the gas in the cavitated tracheid is dissolved. Conifers do exhibit some refilling of cavitated xylem under natural conditions (Sperry and Sullivan 1992; Sperry 1993; Sperry et al. 1994), but the mechanism is not obviously linked to root or stem pressures, which are rare to absent (Kramer and Kozłowski 1979). It is not clear how the natural refilling allows despiration of the torus or whether conifers exhibit substantial cavitation fatigue.

A final wrinkle on pit function occurs in vestured pits. These are convergent in some gnetophytes and angiosperms (Carlquist 1994), with multiple origins in the latter (Jansen et al. 2001). Lignified and compressively strong vestures extend from the pit chamber wall to brace the pit membrane (fig. 5B). This minimizes air seeding by preventing or minimizing membrane distortion (Zweypfennig 1978). The air-seeding pressure will be a function of the same pore diameter that determines the flow resistance—not a larger pore diameter resulting from membrane stretch or rupture. This should permit a greater air-seeding pressure for the same membrane conductivity versus a regular pit, and cavitation fatigue would be prevented. The benefit of vestures would be compromised by their added flow resistance and may only apply to a limited range of air-seeding pressures.

Conduit Size: Tracheids versus Vessels

The single-celled tracheid is the only type of xylem conduit in the fossil record for the first 140 million years of vascular evolution (fig. 1). Within the first 40 million years, by the end of the Devonian, tracheid diameter had already increased to its modern mean maximum of ca. 80 μm (Niklas 1985). During the same time period, the total tracheid area per ground-tissue area increased in association with more complex stelar anatomy (Niklas 1984; Roth-Nebelsick et al. 2000). Increased vascularization was associated with the evolution of leaves (Niklas 1984, 1997) and higher stomatal densities (Beerling et al. 2001). At the same time, CO_2 concentration was plunging along with the physiological range of WUE (fig. 1; Beerling et

al. 2001). The increasingly poor exchange rate of water for CO_2 during this period would make any reduction in the cost of transpiration especially adaptive.

In terms of reducing cost, the increase in tracheid diameter would be more effective than increasing tracheid number. While both strategies reduce dynamic water stress, only the former decreases conduit investment. This is because increasing tracheid diameter causes a fourth-power increase in lumen conductivity, providing much greater flow capacity per conduit (Zimmermann 1983).

The apparent limit on tracheid diameter of near $80\ \mu\text{m}$ may be that greater conduit diameter is only advantageous if accompanied by increased conduit length. The fourth power increase in lumen conductivity with diameter is associated with only a linear increase in surface area available for pits (Calkin et al. 1986). Pit flow resistance becomes limiting unless the pit area can increase via greater conduit length. The pit limitation is most restrictive for circular-bordered pitting and is less so for scalariform pitting (Schulte and Gibson 1988). Wider tracheids are in fact longer—up to a maximum of 10 mm (Schweingruber 1990). Further increases in length and diameter in tracheids may be impossible because of limits to maximum cell volume (Lancashire and Ennos 2002).

Vessels

Being multiple celled, vessels can reach much greater maximum diameters ($500\ \mu\text{m}$) and lengths ($>10\ \text{m}$) than tracheids (Zimmermann 1983). Vessel diameters are not as constrained by a maximum cell volume as tracheids. While wide vessel elements are in fact short, as expected for a volume limit, short elements do not mean short vessels because there is no known limit on the number of elements in a vessel (Lancashire and Ennos 2002).

The advantage of vessels is clear; greater diameter and length permit greater potential hydraulic conductivity per conduit area than the largest of tracheids. Vessels increase the maximum hydraulic conductivity per wood area by two orders of magnitude over tracheids. On a conductivity per leaf area basis, the improvement is a factor of 1.5 orders of magnitude (fig. 2). This reduces the cost of transpiration, increasing the profit margin of the carbon-for-water exchange.

The greater efficiency of vessels is manifest not just in higher conductivities per leaf or wood area compared with tracheids. In many species, conductivities on this basis are equal or even lower in vessel versus tracheid-based woods (fig. 2). The advantage of vessels is in maintaining these conductivities with less total conduit area.

In free-standing trees, vessels make fibers and storage parenchyma in the secondary xylem possible without sacrificing hydraulic conductivity on a wood-area basis. Fibers allow much higher wood densities to be achieved in vessel-bearing versus tracheid-bearing wood (fig. 6), hence, the hardwood versus softwood terminology. The mechanical advantage of increased density is a higher flexural stiffness—less deformation by bending for a given load (Vogel 1988). Greater flexural stiffness may lead to more architectural options; the spreading “decurent” crowns of hardwoods versus the “excurrent” crowns of softwoods (Zimmermann and Brown 1977) may reflect the greater stiffness possible in hardwoods. Vessels also

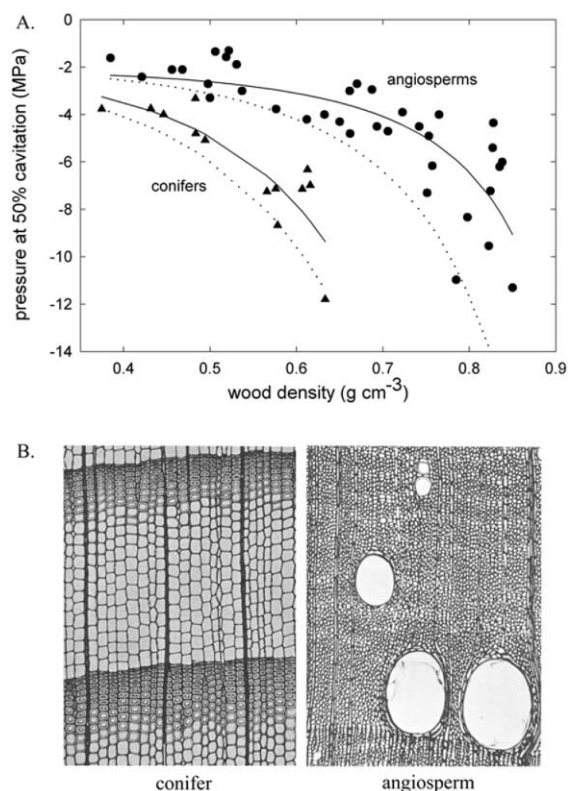


Fig. 6 A, Xylem pressure causing a 50% loss of hydraulic conductivity by cavitation versus wood density for the same angiosperm (circles) and conifer (triangles) stem woods shown in fig. 4B. Solid line indicates curve predicted from the $(t/d)^2$ relationship in fig. 4B. Dotted lines suggest a boundary line below which woods cannot exist because of conduit implosion. Conifers achieve a given cavitation resistance with roughly 50% of the wood density of angiosperms. From Hacke et al. (2001a). B, Sample wood cross sections of a conifer versus an angiosperm. Fibers in angiosperms allow for much higher maximum wood density in hardwoods versus softwoods. However, the density of the fiber matrix seems to parallel the implosion requirement of the vessels, giving the relationship in A. Images from Panshin and de Zeeuw (1970).

make vines possible by packing a given conductivity in a smaller stem area. The 100-fold greater xylem conductivity per wood area of lianas versus gymnosperms (fig. 2) means that a tracheid-based “vine” stem would have to be 10 times thicker than a vessel-based one to achieve the same stem conductivity, i.e., as thick as a free-standing tree!

Given the advantages of vessels, it is not surprising that they have probably evolved independently in five different plant groups (fig. 1; Baas and Wheeler 1996). The earliest fossil vessel element is from vinelike species of Gigantopteridales from the late Permian. The foraminiferous perforation plates of these vessels are very similar to those in modern gnetophytes and are thought to have evolved from tracheids with circular-bordered pits (Li et al. 1996). In contrast, the earliest definitive angiosperm vessels do not appear until the mid-Cretaceous. Scalariform perforation plates may indicate that angiosperm vessels evolved from tracheids with scalariform pitting, as seen

in the presumably ancestral vesselless angiosperms (Baas and Wheeler 1996; Feild et al. 2002).

The origin of a new grade of xylem conduit in conjunction with an all-time low in CO₂ concentration and WUE during the late Carboniferous and early Permian is suggestive of cause and effect. Although vessels would be advantageous even in the absence of CO₂ fluctuation, the heightened requirement for cost-effective water transport would presumably accelerate their evolution. Developmentally and physiologically, the shift from a cambium producing tracheids to one producing vessel elements plus fibers may be simple, requiring shifts in auxin and gibberellin levels during differentiation (Aloni et al. 2000).

A second drop in CO₂ during the Cretaceous (fig. 1) has been linked to the rise and diversification of the angiosperms (Robinson 1994; McElwain et al. 2004), but vessel-based xylem per se may not be directly responsible since it was already present in the Permian Gigantopterids. Reproductive innovations likely played a major role in angiosperm radiation (Cretet and Friis 1987).

Advantages of Tracheids and Small Conduits Generally

The fact that many widespread and dominant plants lack vessels (fig. 1) and that angiosperms appear to have reverted back to a vesselless condition at least once (Young 1981; Baas and Wheeler 1996; Feild et al. 2002) indicates that the advantages of vessels are not universal. Similarly, although maximum vessel lengths and diameters are much greater than tracheids, vessels with lengths and especially diameters within the tracheid range are common, and tracheids operate side by side with vessels in some woods (Carlquist 1988). Even in an axis with very long and wide vessels, most vessels are narrow and short—often less than 1 or 2 cm long (Zimmermann and Jeje 1981).

There are many tracheid myths. Numerous authors have stated that tracheids are superior in terms of resisting cavitation by water stress (Judd et al. 2002; McElwain et al. 2004). This is incorrect; there is no difference between the cavitation pressure of conifers as a group compared to angiosperms (fig. 4). It is also often implied that wider conduits are necessarily more vulnerable to water stress-induced cavitation than narrow ones (Mauseth 1998), aside from identity as tracheids or vessels. However, there are numerous examples of wide conduits that are equally if not more resistant to cavitation by water stress than narrow conduits (Pockman and Sperry 2000). Pit function determines cavitation resistance, not lumen diameter. It is also tempting to say that in situations where freezing is common during the growing season, the generally narrow tracheid would be superior (Feild et al. 2002). However, narrow vessels are as immune to freezing-induced cavitation as narrow tracheids (Davis et al. 1999) and yet can be more hydraulically efficient by being longer.

Narrow and short tracheid-like conduits may have an advantage in being more readily refilled once cavitated because the gas emboli will have a smaller volume and a larger surface-to-volume ratio (fig. 7; Ewers 1985). Although the torus-margo pit structure may prevent some modes of refilling in conifer tracheids, conifers do refill as noted above, and tracheids of seedless vascular plants and vesselless angiosperms have capillary-sealing pits.

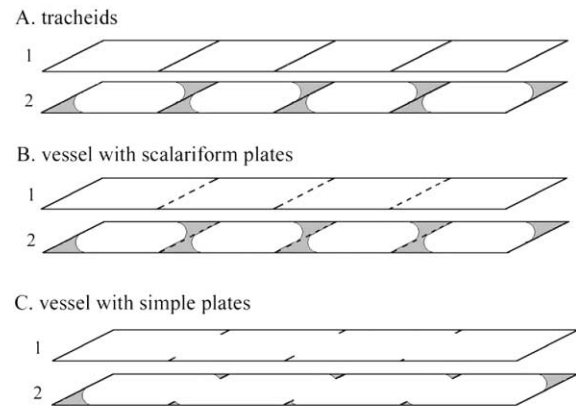


Fig. 7 A, File of four embolized tracheids when (1) fully embolized at negative water potential and (2) partially embolized and refilling at water potentials near or above atmospheric. B, Vessel of four vessel elements with scalariform perforation plates under conditions 1 and 2. C, Vessel of four vessel elements with simple perforation plates under the same two conditions (see Sperry 1986).

An important advantage of tracheid-based conifer trees is that they can achieve a greater cavitation resistance (not conductivity) at lower investment in wall material than vessel-bearing wood (Hacke et al. 2001a). For the same cavitation resistance, conifer stem xylem is roughly 50% lighter than that of angiosperms (fig. 6A). Greater cavitation resistance requires stronger implosion-resistant conduits with more wall material per unit volume (fig. 4) and, hence, denser wood. This relationship holds even in angiosperm wood where fibers are present. The density of the fiber matrix is related to the cavitation resistance of the vessel network, perhaps to mechanically buffer vessels from bending stresses as hypothesized for the primary axes of seedless vascular plants (Vincent and Jeronimidis 1991). The presence of fibers, however, shifts the density versus cavitation resistance relationship in angiosperms to a much higher density range.

Although conifers cannot exploit the advantages of denser wood for increased flexural stiffness, they can tolerate stressful conditions more economically. As the redwoods prove, lower densities of softwoods do not limit height growth. Maximum buckling heights depend on the elastic modulus of wood divided by density—a ratio that is approximately constant across woods (McMahon 1973). Although the tracheid-based system is less hydraulically efficient than a vessel-based one (fig. 2), when stress tolerance is more important than high gas-exchange rates, the greater economy of cavitation resistance in tracheid-based woods may be beneficial. It would be very interesting to learn if this advantage extends to the vesselless angiosperms because, together with potentially greater ease of cavitation reversal, it might have played a role in the reversion to the vesselless condition.

Vessel Perforation Plates

Within angiosperm vessels, the long-held notion that scalariform perforation plates are ancestral to simple perforation plates, representing the vestiges of hydrolyzed scalariform pit-

ting between tracheids (Bailey and Tupper 1918), is supported by recent phylogenies. However, the persistence of scalariform plates in many lineages and the proposed reappearance of these plates in yet other lineages suggests an adaptive function of this intermediate morphology (Baas and Wheeler 1996). This advantage must balance the added flow resistance of scalariform plates, which is 2%–20% of vessel element flow resistance versus 2%–5% for simple plates (Schulte and Castle 1993; Ellerby and Ennos 1998).

Scalariform perforation plates may couple the advantages of vessels with the refilling capability of smaller conduits (fig. 7; Sperry 1986). When the xylem pressure in an embolized vessel with scalariform plates rises to near atmospheric pressure, water is wicked across the narrow perforations, dividing up previously continuous gas space into smaller bubbles—one to each vessel element. These smaller packages may dissolve more rapidly than fewer, larger bubbles in refilling vessels with simple perforation plates. This possible advantage of scalariform perforation plates would apply to any plant that depends on refilling—regardless of whether this cavitation was caused by freezing or water stress. It is a more universal advantage than the putative role of scalariform plates in minimizing freezing-induced cavitation (Zimmermann 1983) and may explain the presence of this plate type in both tropical and temperate climates (Baas and Wheeler 1996).

The Conduit Network

An essentially universal pattern among extant plants is that the major flow resistances are localized to highly branched downstream ends of the flow path (Tyree and Ewers 1991). This is associated with a gradual narrowing of conduit diameters moving downstream in the shoot (Zimmermann 1978). This pattern has at least four important advantages: (1) it minimizes differences in water supply to leaves throughout the canopy and maintains similar dynamic water stress and gas-exchange capacity (Zimmermann 1983); (2) it minimizes the increase in total flow resistance with increasing tree height, an important adaptation in the competition for light (Becker et al. 2000; Enquist et al. 2000); (3) it allows for the hydraulic dominance of leaders versus lateral branches—the hydraulic expression of apical dominance (Ewers and Zimmermann 1984a, 1984b); and (4) it limits hydraulic failure to minor branches. Hydraulically “subservient” branches cavitate first under stress, effectively reducing the load on more valuable portions of the system (Tyree and Sperry 1988). Localizing short conduits to the ends of the flow path prevents cavitation from spreading into major transport arteries where longer conduits maximize conductivity (Comstock and Sperry 2000). The system operates like an electrical circuit network with designed failure points—hydraulic fuses—that limit the consequences of an overload (Sperry et al. 2002).

Network-level adaptations have been observed in seedless vascular plants and fossil plants, indicating an early origin. *Psilotum nudum* exhibits a decline in tracheid diameter and branch hydraulic conductivity with more distal branch rank (Schulte et al. 1987). The fossil *Psilophyton dawsonii* exhibits low conductivity branch junctions that could have been important in localizing cavitation to peripheral branches (Niklas and Banks 1985). The evolution of apical dominance from

ancestral dichotomous branching may have been associated with the ability to vary conductivity relative to transpiring area, in that dominant branches would require a proportionally greater conductivity than laterals.

An important optimization criterion at the network level is to maximize the hydraulic conductance to all transpiring surfaces while keeping the overall conduit investment at a minimum. Murray’s law is a good general test of this criterion, predicting that maximum hydraulic conductivity per network volume will be achieved by keeping the sum of all conduit radii raised to the third power constant across branch ranks (Murray 1926; Sherman 1981). It holds in angiosperm xylem under situations where xylem conduits are not functioning directly in mechanical support (Canny 1993; McCulloh et al. 2003). Moreover, these plants tend to produce fewer wider conduits at the stem base and more narrower conduits distally, a configuration that maximizes the Murray law optimum versus a system with equal numbers of conduits at each level and that also localizes major flow resistance to the periphery (McCulloh et al. 2003).

Conclusion

Xylem structure has been regarded as a conservative trait, tending to track phylogenetic lineages, and by implication, having weak or neutral adaptive significance (Carlquist 1988). While this may be true of some traits, it is clear that many basic features—conducting tissue itself, conduit type, pitting type, and perforation plate type, to reiterate a few examples—are subject to convergence and reversal. These patterns imply a strong adaptive significance, the nature of which presumably maximizes the difference between carbon uptake during transpiration and carbon expenditure on supplying the transpiration stream.

A central challenge to interpreting the adaptive significance of water-transport traits is to be able to better predict the optimal carbon-for-water exchange. It exists; it is context dependent with multiple optima depending on circumstances, but it is difficult to specify (Cowan 1977; Givnish 1986). One barrier is the elusive cost of transpiration. This depends in part on quantitative structure-function relationships in the xylem. Although some of the relevant trade-offs have been identified here—between safety from cavitation, hydraulic conductivity, conduit investment, mechanical support, and cavitation repair—the often speculative understanding of each trade-off becomes useless when all must be integrated in a single-functioning system to estimate the cost-benefit margin. More pieces of the puzzle will fall into place as structure-function trade-offs are quantified in extant plants and incorporated in integrative analyses of the carbon-for-water exchange.

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