

Hydraulics of Vascular Water Transport

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Abstract The science of plant water transport is equal parts of physics and biology. Plants have evolved a complex wick system that harnesses the cohesive hydrogen bond energy of liquid water and suppresses the heterogeneous nucleation of cavitation. Trade-offs between making the wick safe against cavitation and implosion, yet efficient in moving water, result in the process being limiting to plant performance. Cavitation limits the range of negative pressures that can be harnessed to move water, and the hydraulic conductance of the wick limits the flow rate that can be moved at a given negative pressure gradient. Both limits constrain CO₂ uptake via the water-for-carbon trade-off at the stomatal interface. Research in the area concerns the mechanisms of cavitation, its reversal by embolism repair, consequences for plant ecology and evolution, and the coupling of water transport to plant productivity. Very little is known of the molecular biology underlying xylem physiology.

1 Introduction

Few transport processes generate more controversy and misunderstanding than the long-distance movement of water in the xylem of plants. The transport mechanism is very simple and very remarkable – remarkable enough to be contentious. In its essentials, it is a physical process. Yet the physics impose major constraints on the biology of plants. This chapter explains water transport and identifies issues where research is active or needed. It is written to be accessible for the nonspecialist.

Of all biological transport systems, plant xylem transports the most fluid over the longest distances (Vogel 1994). A tree with a trunk the size of a man's waist transports on the order of 100 l of water on a clear day (Enquist et al. 2000). Summing over a watershed, plant water use matches the runoff in rivers, and constitutes just under half the annual precipitation (Schlesinger 1997). This conspicuous consumption makes water a major limiting resource for plant life. What is

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all this water used for? A miniscule percentage, less than 1%, is split in the photosynthetic reaction to release O_2 . A few more percentage points are pulled into cells by osmosis in the growth process (see chapter "Plants as Mechano-osmotic Transducers"). The remaining bulk, usually over 95%, is evaporated to the atmosphere through open stomata: the process of transpiration (Sutcliffe 1968). If vascular plants could exist without stomata, plants would not be water-limited and arid and semi-arid landscapes would be far more productive.

But, plants need stomata to let in sufficient CO_2 for photosynthesis, and so they must transpire. The exchange rate of water for carbon is very poor, with hundreds of molecules of water lost per molecule of CO_2 fixed under typical conditions. The transpiration stream represents a river of water flowing in exchange for a relative trickle of carbon.

2 The Cohesion–Tension Transport Mechanism

With such a poor exchange rate of water moved per unit carbon acquired, plants had to evolve an energetically cheap transport process to avoid starvation. It is hard to imagine a more economical process than the prevailing "cohesion–tension" explanation (Pickard 1981). According to this mechanism, water is wicked up the plant. Like a wick, the plant sucks fluid to a porous evaporating surface by capillary force. It is a physical process that operates without the need for metabolic energy once the anatomically complex "wick" system has been grown.

The essential physics of the wick are illustrated in Fig. 1a. Water evaporates from a meniscus that is anchored by capillary forces in a tube. These forces are the adhesion of water to the hydrophilic tube and the surface tension of water. Because the meniscus is held in a relatively stationary position as water evaporates from its surface, the pressure in the liquid water drops, and the evaporated molecules are replaced by bulk flow towards the meniscus (Rand 1978). The energy source is the vapor pressure deficit that initiates evaporation. The energy for evaporation is transferred to the hydrogen bonds that generate the capillary forces anchoring the meniscus. Hydrogen bond energy creates the drop in water pressure which drives flow up the tube.

Although energetically efficient for the plant, the cohesion–tension mechanism is limited in the subatmospheric water pressure that it can generate. This pressure, P , is usually expressed relative to atmospheric and is a negative value. One theoretical limit to P is "capillary failure" of the forces holding the meniscus in place. The most negative pressure the meniscus can generate without giving way, P^{CAP} , is given by the capillary equation:

$$P^{CAP} = -4T \cos(a)/D_c, \quad (1)$$

where T is the surface tension of water, a is the contact angle between water and the tube wall (a measure of wettability or adhesion), and D_c is the diameter of the

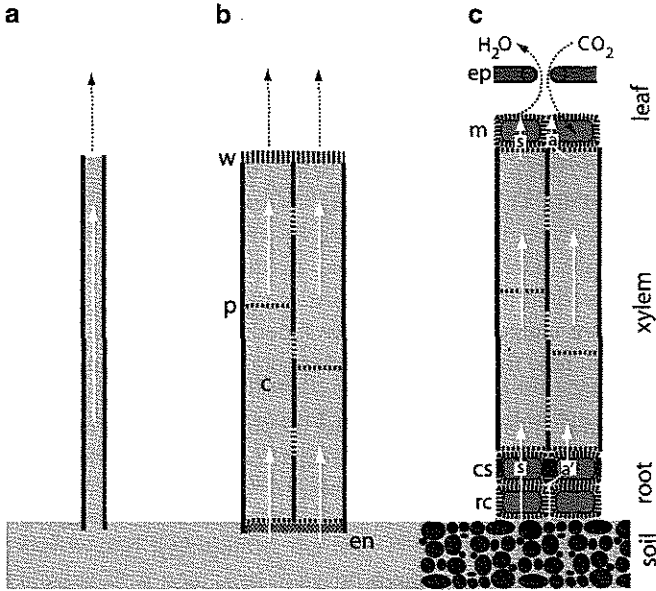


Fig. 1 The cohesion–tension mechanism for transpiration-driven xylem flow. (a) The basic wicking process: evaporation from a meniscus coupled to bulk flow by capillary forces. (b) In plants, large capillary suction is generated in narrow pores of cell walls (*w*) and long-distance bulk flow occurs in a low-resistance network of dead xylem conduits (*c*). Conduits are connected by pits (*p*), which also protect against air-entry and embolism in the inevitable event of damage to individual conduits. Water is filtered through living cell membranes at the root endodermis (*en*) by reverse osmosis. (c) Living cells (rounded rectangles enclosed in hatched cell walls) do not generate transpirational flow (*ep* leaf epidermis; *m* mesophyll; *cs* Casparian strip of the endodermis; *rc* root cortex). Water flows through them to the site of evaporation via symplastic (*s* arrows) and apoplastic routes (*a* arrows). In the root, the apoplastic route (*a'*) is interrupted by the Casparian strip. Transpiration is actively regulated by stomatal opening through which the water-for-carbon gas exchange takes place

circular tube holding the meniscus. If P drops to P^{CAP} , the meniscus is pulled inward, emptying the tube by capillary failure.

A second limit on P concerns the boiling point of water. The vapor pressure of water at 20°C is about 2.3 kPa in absolute pressure. At sea level, that yields a potential minimum (most negative) P of -99 kPa at the boiling point. Boiling is generally heterogeneously nucleated by gas bubbles, hydrophobic surfaces, or other materials that destabilize the cohesion of water molecules via hydrogen bonding (Debenedetti 1996). If heterogeneous nucleation is suppressed, boiling will not occur, and liquid water will sustain a P below the boiling point. The water is in a metastable “super-sucked” state: a state equivalent to being super-heated (Debenedetti 1996), except the water pressure is being lowered past the boiling point at ambient temperature. As explained in Sect. 4, P in plant xylem must drop below -99 kPa for water to be extracted from soil and pulled up the xylem against gravity and

friction. Therefore, the cohesion–tension mechanism requires the xylem sap to be in a metastable liquid state.

Water under negative P is often referred to as being under “tension” because the liquid exhibits tensile strength as if it were a solid. In Lyman Briggs’ classic “Z” tube experiments, liquid water placed under tension by centrifugal force sustained a P of below -25 MPa ($-25,000$ kPa) before the abrupt appearance of the vapor phase (Briggs 1950). This abrupt “boiling” is termed cavitation. In Brigg’s experiments, cavitation was probably nucleated by irregularities in the contact between the water and the Z-shaped capillaries. In the absence of any heterogeneous nucleation, theoretical models predict that pure water can develop a P of at least -30 MPa at room temperature before the kinetic energy of the water molecules is sufficient to overcome their cohesion and spontaneously nucleate cavitation (Kwak and Panton 1985).

The biggest threat to metastable water in plant xylem is “bubble nucleation”: cavitation triggered by gas bubbles in the sap (Sect. 6). The most negative P that can be sustained in the presence of an air bubble, P^{BUB} , can be derived from La Place’s law for spheres (Vogel 1988):

$$P^{\text{BUB}} = -4T/D_b, \quad (2)$$

where D_b is the diameter of curvature for the bubble. If P drops below P^{BUB} , the surface tension forces that tend to collapse the bubble are exceeded by the negative P that tends to expand the bubble, and the gas phase grows (Oertli 1971). The similarity of (1) and (2) indicate the central importance of surface tension in limiting the magnitude of P generated by the wicking process.

A third limit to P concerns the strength of the capillary tube itself. The internal fluid is under negative pressure, which can lead to the collapse of a weak tube. The P causing failure by tube implosion, P^{IMP} , is difficult to express in simple equation because it depends on the shape of the tube, the relative thickness of the wall, and the internal structure of the wall, among other things (Young 1989). In the simple case of an isolated cylindrical tube where the wall is isotropic and less than a tenth of the tube radius (e.g., Fig. 1a), La Place’s law for cylindrical hoop stress can be used to estimate P^{IMP} :

$$P^{\text{IMP}} = -2\sigma(t/D_c), \quad (3)$$

where σ is the strength (force per cross-sectional wall area) of the wall against implosion and t is the thickness of the tube wall. While (3) does not apply to actual xylem conduits, it is useful for showing the importance of the “thickness-to-span” ratio (t/D_c) for determining P^{IMP} . The greater this ratio, the stronger the conduit wall, regardless of additional structural complexities in actual conduits (Hacke et al. 2001).

The role of these three potential limits: P^{CAP} , P^{BUB} , and P^{IMP} , in constraining the range of P achievable in plant xylem will be considered after looking at the anatomy of the “wick” grown by plants.

3 The Anatomy of the Flow Path

The anatomy of the flow path couples narrow pores at the site of evaporation, which maximize capillary suction, to much wider water-filled channels in the vascular tissue for maximizing ease of transport. The physical concept is illustrated in Fig. 1b. Living cells of leaves and roots are added in Fig. 1c.

3.1 The Evaporating Surface

The evaporating surface is the cell walls abutting internal air spaces in the leaf or other transpiring tissue. The meniscus of Fig. 1a is located in the nanometer-scale pores of the cell wall, represented by the surface of narrow channels marked "w" in Fig. 1b, and by the leaf mesophyll cell walls labeled "m" in Fig. 1c. Cell wall capillary forces generate the negative P that pulls water up the xylem and out of the soil. Being narrow and hydrophilic, the wall channels can theoretically generate extremely negative P : a wall pore 5 nm in diameter would not exhibit capillary failure until $P^{\text{CAP}} = -58.4$ MPa, assuming a contact angle of zero and a surface tension of 0.073 N m^{-1} (1).

The negative water pressure in the cell wall channels pulls water from the xylem conduits either directly via an apoplastic route of contiguous walls (Fig. 1c, arrow labeled "a"), or indirectly through protoplasts by a symplastic route (Fig. 1c arrow labeled "s"; Canny 1990). In the symplastic route, water is ultimately pulled from the protoplast by reverse osmosis to the site of evaporation at the cell wall surface. Osmosis itself does not power the transpiration stream; it keeps cells hydrated against the negative P of the apoplast. In the absence of transpiration, however, osmotic uptake of water by growing cells will initiate xylem transport (Boyer et al. 1985). Osmosis into the expanding cell exerts an inward pull on the wall menisci, which hold fast and generate negative P for water uptake from the xylem.

3.2 The Xylem Conduits

The xylem conduits (tubes labeled "c" in Fig. 1c) provide a high-conductance pipeline for delivering the transpiration stream to the site of evaporation. Without them, the negative P required to supply transpiration in a plant taller than a few centimeters would stress the plant beyond physiological tolerance (Raven 1987). Xylem conduits are many microns in diameter as opposed to the nanometer-scale cell wall channels. Poiseuille's law for laminar flow (which prevails in xylem) predicts that hydraulic conductivity (flow rate per pressure gradient) is proportional to tube diameter to the fourth power. Consequently, the conductivity through a xylem conduit is many orders of magnitude greater than through cell wall channels.

High conductivity means the pressure gradient of the transpiration stream can be relatively low: ca. 0.01 MPa m^{-1} in trunks and major branches (Zimmermann 1983). Pressure gradients increase as conduits become narrower moving from trunks to minor branches and twigs. The highest gradients appear to be in petioles and leaf veins where they can exceed 10 MPa m^{-1} (Zwieniecki et al. 2002). Modest pressure gradients in the major stems mean that more water can be carried longer distances without requiring extremely negative P . The total pressure drop required to pull the transpiration stream against friction is often around 1 MPa ($1,000 \text{ kPa}$) in angiosperms, and somewhat greater in conifers (Mencuccini 2003).

In keeping with the physical basis of transport, the xylem conduits function after they die and lose their protoplasts. They are cell wall skeletons, with thick secondary walls that are rigidified by lignin to minimize the risk of implosion by negative sap pressure (3). The thick walls help maximize the “thickness to span” ratio (t/D_c). The lignification and layering of the secondary wall maximizes wall strength (σ). Increases in both of these variables make P^{IMP} more negative (3), and provide greater protection from conduit implosion.

The ancestral type of conduit, the tracheid, is a single elongated cell several millimeters long. Most seedless vascular plants and gymnosperms function with tracheids only. Angiosperms and gnetophytes (and some ferns) have the derived vessel type of conduit. Vessels consist of many unicellular vessel members joined by perforation plates to form a multicellular tube several centimeters long. Tracheids evolved into vessel members to give rise to vessels (Bailey and Tupper 1918).

Importantly, as the conduits mature and lose their protoplasts to become functional, they start out full of fluid. If not, their lumens would be unable to generate sufficient capillary suction to fill themselves with water in most conditions. Because the lumen diameter is many microns, the P^{CAP} of the conduit lumen is only a few kPa negative (1) which is much less negative than the mid-day P of the transpiration stream. Although capillary forces are responsible for driving the transpiration stream, capillary *rise* is not involved. The conceptual wick in Fig. 1c cannot function unless it is primed by being water-filled. In the event that conduits do become gas-filled, many species have mechanisms for actively pumping water into empty conduits (see Sect. 8).

All vascular systems have to minimize impacts of the inevitable leaks that occur. Leaks in the transpiration stream are inward. If a xylem conduit is damaged, the transpiration stream does not pour out because it is under subatmospheric pressure. Instead, air leaks into the conduit. The impact of leaks is minimized by the presence of multiple conduits in parallel and in series. The conduits are coupled by interconduit pits that act as “check valves” allowing passage of water but resisting passage of an air–water interface (dashed openings labeled “p” in Fig. 1b). Air is thereby inhibited from spreading from a gas-filled (“embolized”) conduit (Zimmermann 1983). Whether the network is plumbed by tracheids or vessels, the basic compartmentalization represented in Fig. 1b is preserved; the only difference is in the size of the compartments and details of the interconduit pitting.

3.3 Soil Water Uptake

The network of overlapping conduits extends to the roots where the negative P pulls water from the soil (Fig. 1c). As in the leaves, there is a symplastic (Fig. 1c, "s" arrow) and apoplastic (Fig. 1c, "a" arrow) route for water to move across the root cortex (cell layer "rc" in Fig. 1c; Steudle 1994). At the endodermis, however, (and in some plants also at the exodermis) most water is forced through cell membranes because of the Casparian strip which forms an apoplastic barrier (Fig. 1c, "cs"). Under transpirational conditions, the water is pulled across the membranes by reverse osmosis. The endodermal filter (hatched zone labeled "en" in Fig. 1b, cell layer labeled "cs" in Fig. 1c) allows the plant to control the content of the transpiration stream. When transpiration is negligible, and the soil is wet, the endodermis can allow water to move into the xylem by osmosis, creating positive "root pressure" in the xylem (Steudle 1994).

Soil water is also usually under a negative P , and for the same reason as in the plant: capillary forces holding water in pore spaces (Fig. 1c, "soil"). The cohesion-tension mechanism can be summarized as a tug-of-war on a rope of water between capillary forces in cell walls versus soil.

4 The Magnitude of Xylem Water Pressure (P)

Most textbook descriptions of water transport in plants emphasize the need to pull water against the force of gravity. The hydrostatic slope is -9.8 kPa m^{-1} (20°C , 45° latitude, sea level). Hence, a 10-m tall tree must have xylem pressure of -98 kPa just to counteract gravity (Vogel 1988). This is near the boiling point of water (-99 kPa at sea level), a fact which excites controversy, because trees can be much taller than 10 m. Obviously, for the cohesion-tension mechanism to work, heterogeneous nucleation of boiling (cavitation) must be suppressed in the xylem conduits and cell wall pores.

Gravity actually exerts a relatively trivial influence on xylem P . As mentioned above (Sect. 3.2), about 1,000 kPa of pressure is required to move water from soil to leaves against friction, a value that does not appear to be markedly size-dependent. Overcoming friction and gravity requires a 10-m tall tree at mid-day to have a xylem pressure of about $-1,100 \text{ kPa}$, or more conveniently, -1.1 MPa . The other significant determinant of xylem pressure is the soil water potential. Because of the reverse osmosis at the root, the xylem must extract water not only from the soil pore space, but also against the osmotic strength of the soil solution. A 10 m mangrove rooted in seawater must pull against ca. -2.4 MPa of osmotic potential, which added to -1.1 for gravity and friction, comes to -3.5 MPa . In deserts, plants have to pull against soil water potentials of -5 MPa or lower. The lowest xylem pressure the author is aware of is -13.1 MPa (mean value) in a shrub from the California chaparral (*Ceanothus cuneatus*) during the dry season (Jacobson et al. 2007).

5 The Limits to Negative Pressure (P) in Xylem: "Vulnerability Curves"

How low can xylem pressures drop before xylem transport fails? This question strikes at the heart of the cohesion-tension mechanism, because for it to work, water pressures must be able to become sufficiently negative to extract water from soil and move it against gravity and friction.

"Vulnerability curves" provide the answer for how low the sap pressure can drop before water transport fails (Tyree and Sperry 1989). These curves show the hydraulic conductivity of the xylem as it is exposed to progressively more negative pressures. Curves from stem xylem of three species are shown in Fig. 2. The conductivity is expressed as the percentage loss from the initial value (PLC). The range of pressure causing vascular dysfunction is from where PLC first becomes significant to where it reaches 100. At 100 PLC, enough xylem conduits have become nonfunctional to stop transport completely. The loss of conductivity is generally gradual, indicating that some conduits in the stem are more vulnerable than others.

The species in Fig. 2 differ in their vulnerability to failure, but all can generate sufficient negative pressure to function by the cohesion-tension mechanism in their environment. Cottonwood (*Populus fremontii*), the most vulnerable species, begins to fail between -1.0 and -1.25 MPa. But it grows in riparian environments where soil water potentials are always near zero. It needs less than -1.25 MPa of negative pressure to move water against friction and gravity (Pockman and Sperry 2000). In contrast, hoary-leaf ceanothus (*Ceanothus crassifolius*) is the most resistant to failure. It grows in seasonally very dry chaparral of southern California where it

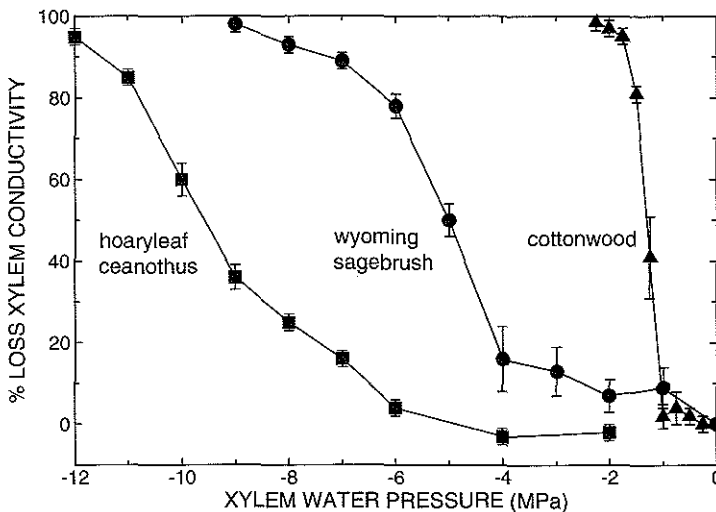


Fig. 2 Vulnerability curves of stems from hoaryleaf ceanothus (*Ceanothus crassifolius*), wyoming sagebrush (*Artemisia tridentata* var. *wyomingensis*), and cottonwood (*Populus fremontii*). From Sperry (2000)

needs very negative pressure (to -11 MPa or lower) to extract water from dry soils (Davis et al. 2002). The sagebrush (*Artemisia tridentata*) is intermediate, and grows in environments intermediate in stress (Kolb and Sperry 1999). It appears to be a general rule that vulnerability to vascular failure correlates with the physiological range of P required by a plant in its habitat (Maherali et al. 2003).

Vulnerability curves can be measured in a variety of ways. The ones in Fig. 2 come from the centrifugal force method (Pockman et al. 1995). This technique adapts Lyman Brigg's "Z-tube" experiments on capillary tubes to plant xylem. Stems are spun in custom rotors to put the xylem water under tension, and the conductivity of the stem is measured either during spinning (Cochard 2002) or between bouts of spinning using a hydraulic head (Alder et al. 1997). The two approaches appear to give similar results (Li et al. 2008). A more tedious, but more natural method is to dehydrate plants or plant parts to different pressures measured using either a pressure bomb or psychrometer (Sperry 1986). Conductivity is measured on stem pieces cut under-water (to avoid inducing embolism) and expressed relative to either the nonstressed value or to a maximum value obtained after flushing the stem to reverse in situ embolism. This "dehydration" method generally matches centrifugal techniques (Pockman et al. 1995).

5.1 Freeze-Related Dysfunction

Freeze-thaw cycles can also induce xylem dysfunction as illustrated in Fig. 3a for water birch (*Betula occidentalis*). The dashed line is the room temperature "water

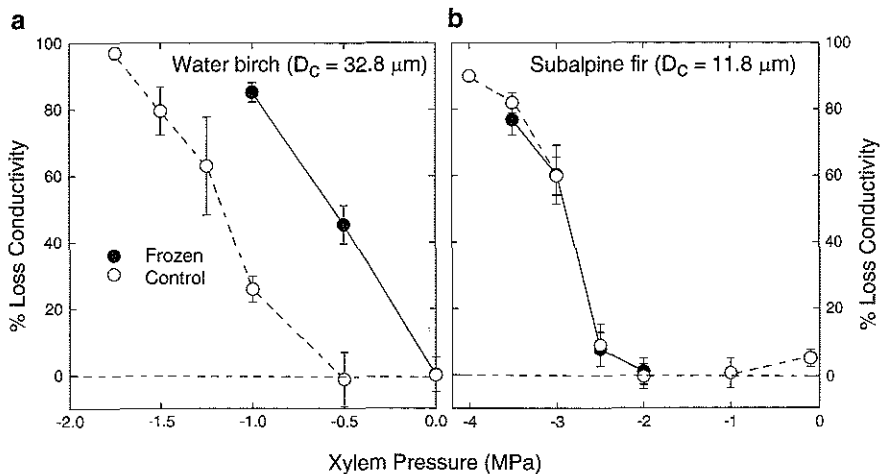


Fig. 3 Vulnerability curves with (solid symbols, lines) versus without (open symbols, dashed lines) a freeze-thaw cycle at each xylem pressure. Freeze-thaw cycles induce additional dysfunction in some species (a, Water birch, *Betula occidentalis*) but not in others (b, subalpine fir, *Abies lasiocarpa*, D_c = mean xylem conduit diameter). From Sperry and Sullivan (1992)

stress" vulnerability curve ("control", open symbols), indicating a threshold of between -0.5 and -1.0 MPa for the onset of failure. The curve was produced using the centrifugal force method. The solid line is a "freeze-thaw" curve ("frozen," solid symbols), representing stems that were frozen and thawed in the centrifuge at the indicated xylem pressure. The freeze-thaw treatment caused much more dysfunction in this species than water stress alone. Species differ in their response to freeze-thaw cycles. In contrast to birch, stems of sub-alpine fir (*Abies lasiocarpa*) shown in Fig. 3b show no additional failure caused by the freezing treatment (Sperry and Sullivan 1992). Numerous studies have documented naturally occurring loss of xylem conductance associated with freeze-thaw events in nature (Cavender-Bares 2005).

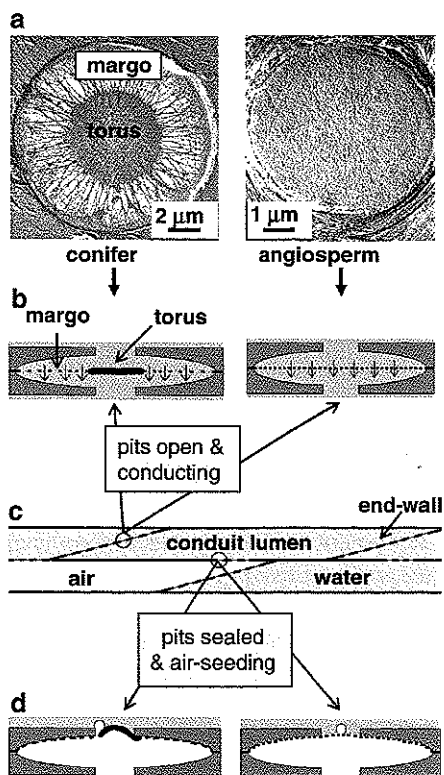
6 Causes of Limits to Negative Xylem Pressure (P)

Vulnerability curves support the cohesion-tension mechanism. They indicate that nucleation of cavitation can be suppressed and metastable water can exist. Negative pressures in xylem are sufficient to pull water from soil, against friction and gravity, to the site of transpiration. But the curves also show that P is limited. What limits P ?

Research has documented xylem dysfunction by all three modes: capillary failure ($P < P^{CAP}$), bubble-nucleation ($P < P^{BUB}$), and implosion ($P \leq P^{IMP}$). Implosion appears to be the rarest cause of dysfunction, having been observed only in the axial tracheids of pine (*Pinus*) needles (Cochard et al. 2004), transfusion tracheids of *Podocarpus* (Brodribb and Holbrook 2005), vessels of *Eucalyptus* species (Cuevas 1969), and vessels of cell-wall mutants in tobacco (Piquemal et al. 1998). In *Pinus* and *Podocarpus*, the implosion is known to be reversible, with buckled walls at or below P^{IMP} recovering their original shape with rehydration as P rises back above P^{IMP} . In most species, implosion has not been observed, and dysfunction is caused by cavitation and gas-phase embolism before P can reach P^{IMP} . Estimated safety factors from implosion (P^{IMP}/P at failure) range from 1.9 for angiosperm vessels to 6.8 for the tracheids of conifer stem wood (Hacke et al. 2001).

Much research points to gas bubbles as the culprits that trigger cavitation and break the water column in nonimploding conduits. Under water-stress conditions, bubbles are pulled into the functional conduits by the "air-seeding" process (Zimmermann 1983). As sap pressures become increasingly negative in a water-filled conduit, air is pulled through the interconduit pits from previously embolized conduits (Fig. 4d; Crombie et al. 1985; Sperry and Tyree 1988). In many cases, the air enters by capillary failure at the pit membrane [$P < P^{CAP}$, (1)]. Once inside the water-filled conduit, the bubble can seed the phase change to vapor [$P < P^{BUB}$, (2)] and the water pressure rises abruptly to near atmospheric (Shen et al. 2002). The gas void expands to fill the entire conduit as water is drained by the transpiration stream flowing through adjacent conduits. Air-seeding could also occur through microfractures in the conduit wall created by incipient implosion (Jacobsen et al. 2005),

Fig. 4 Structure and function of interconduit pits in conifer tracheids (*left*) and angiosperm vessels (*right*). (a) Pit membranes, *face view*. (b) *Side view* schematic of membranes within the pit chamber formed by the secondary walls. Pits open and functioning in water transport. (c) Schematic of pit location within conduit network. (d) *Side view* of pits in sealed position showing proposed air-seeding process. From Pittermann et al. (2005)



or from microbubbles trapped in wall crevices (Pickard 1981; Shen et al. 2002), but there is no evidence for either mechanism.

The air-seeding process described above requires an embolized conduit to begin with, but embolism by damage is inevitable. Conduits become air-filled from leaf abscission, branch breakage, insect feeding, or even protoxylem rupture during tissue growth. Although the pits evolved to prevent leakage from embolized conduits, they also evolved to pass water freely. These two functions are in conflict, and consequently these pit valves appear to be the Achilles' heel of the pipeline.

The fact that cavitation can be caused by air entry into the xylem conduits makes it possible to measure vulnerability curves using positive air pressure rather than negative sap pressure (Cochard et al. 1992). In the "air-injection" method, a hydrated stem with xylem pressures at atmospheric is injected with air at progressively greater pressure, and the effect on hydraulic conductivity is measured. In this experiment, air is being pushed into the xylem rather than being pulled by negative sap pressure. As expected, air-injection curves generally agree with other vulnerability curve methods that use negative xylem pressure (Sperry et al. 1996).

Air-seeding is not the only source of bubbles in the xylem sap. According to the "thaw-expansion" hypothesis, freeze-thaw cycles create air bubbles that potentially

trigger cavitation (Sucoff 1969). Gases are practically insoluble in ice, and tend to freeze out in bubbles as the sap freezes. If the sap pressure is negative enough, the bubbles will nucleate cavitation. “Negative enough” means P is less than $P^{\text{BUB}} = -4T/D_b$, where D_b is the bubble diameter [(2); Yang and Tyree 1992]. In support of the hypothesis, experiments under controlled conditions where transpiration is negligible have shown that it is indeed the thawing phase that creates the cavitation and not the freezing phase (Mayr and Sperry 2010). Furthermore, water that is super-saturated with air creates much more cavitation after a freeze–thaw cycle than water at an equilibrium gas concentration (Sperry and Robson 2001). Bubble nucleation according to the thaw-expansion mechanism is assumed to cause transport failure associated with freeze–thaw cycles (Fig. 3a).

7 Anatomy of Cavitation

Textbooks often remark that larger conduits are more vulnerable to cavitation, but the reality is much more complex, and in many cases not well resolved. Although a size-by-vulnerability trend can be found for cavitation by water stress (Fig. 5a), it is generally statistically weak and often not significant depending on the sample size and species composition (Tyree et al. 1994; Pockman and Sperry 2000; Hacke et al. 2006). An ambiguous dependency on conduit size is not surprising, because the vulnerability to air-seeding should depend on the structure of the interconduit pits rather than the dimensions of the conduit.

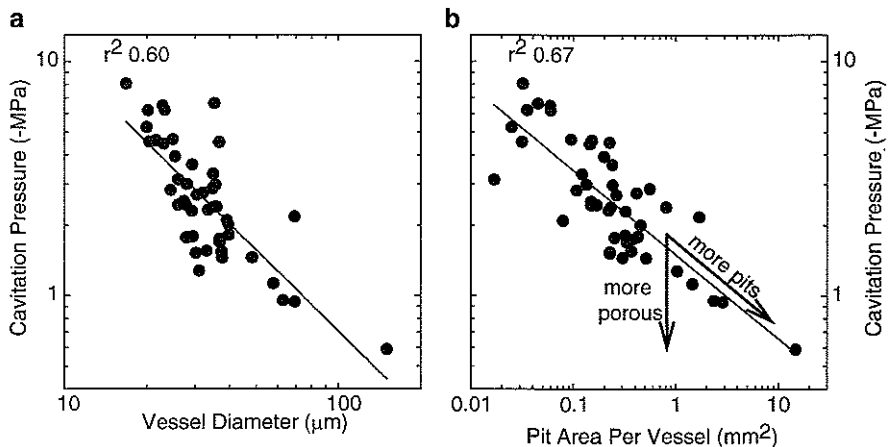


Fig. 5 Average cavitation pressure versus average vessel diameter (**a**) and average pit area per vessel (**b**) in angiosperms. Data points are species averages, compiled from Hacke et al. (2006), Christman et al. (2009), Christman and Sperry (2010)

7.1 Pit Valve Structure and Function

Interconduit pits are thin areas where secondary wall has not been deposited (Fig. 4). Only the primary walls divide the adjacent conduits, forming a thin sheet of cellulosic meshwork termed as pit membrane. In most plants (excepting most gymnosperms), the pit membrane is homogenous: uniformly thin and microporous (Fig. 4a, right). The pores in this membrane form a capillary seal and inhibit air entry. Air-seeding appears to occur by capillary failure rather than membrane rupture (Fig. 4d, right). If the air bubble is large enough to nucleate cavitation [(2); Shen et al. 2002], the pressure will relax to atmospheric and the gas void will grow to fill the entire conduit as water is drained out by the transpiration stream. According to (1), larger pores (bigger D_c = pore diameter) will make for leakier pit membranes and more vulnerable xylem.

What complicates this simple conclusion is that most membrane pores are much smaller than those indicated by the cavitation pressure of a stem (Choat et al. 2008). Pores of air-seeding size are apparently quite rare, which suggests a role for probability. A single angiosperm vessel can have 10,000 or more interconduit pits (Christman et al. 2009). No matter how faithfully the developmental program is performed, not all of these pits will be the same. Of the thousands of pits that might be holding out the air from an adjacent embolized vessel, it only takes one leaky membrane to compromise the seal. The more pits there are, the leakier will be the seal by chance. Indeed, there is a tendency for more vulnerable angiosperm xylem to have a greater extent of pitting per vessel (Fig. 5b, “more pits” arrow; Wheeler et al. 2005). This may also underlie the tendency for bigger vessels to be more vulnerable to cavitation (Fig. 5a): because they tend to have more pits.

Pit structure may also influence the probability of leaky membranes in a vessel. Species with thinner membranes tend to be more vulnerable to air-seeding (Choat et al. 2008). Fewer layers of cellulose microfibrils may increase the chances of creating thin spots or large holes during pit membrane development. For a given number of pits, thinner and more porous membranes would tend to increase vulnerability (Fig. 5b, “more porous” arrow). The consensus is that it is the combination of individual pit structure and pit number that determines vulnerability to cavitation by air-seeding (Fig. 5b, “more pits” and “more porous” arrows).

A related problem is the difficulty of measuring the vulnerability of large-vessel species like ring-porous trees, many tropical trees, and lianas. Centrifuge and air-injection methods generally indicate that many large vessels are exceptionally vulnerable, with some cavitating at a negative P of only a few tenths of an MPa (Li et al. 2008). Some field studies also show many large vessels are not functioning at mid-day (Taneda and Sperry 2008). However, long vessels may cause artifacts in at least some centrifugal force techniques. Long vessels allow microbubbles or other nucleators to enter the center of the stem that is placed under tension, causing premature cavitation (Cochard et al. 2005). More techniques need to be brought to bear on cavitation including Magnetic Resonance Imaging (MRI) and single-vessel measures of air-seeding pressures (Holbrook et al. 2001; Choat et al. 2005).

Conifers and most gnetophytes have a different kind of interconduit pit (Fig. 4, left). The pits are uniformly circular, and rather than having a homogenous membrane, the center of the membrane is greatly thickened to form a "torus" (Fig. 4a, left). Surrounding and holding the torus is a very porous "margo." To seal against air entry, capillary forces at the large margo pores, though relatively weak, are strong enough to aspirate the membrane, sealing the thick torus over the pit aperture (Fig. 5d, left). Air-seeding through torus-margo pits seems to occur by slippage of the torus from sealing position, exposing (and perhaps even rupturing) the margo whose pores are too large to prevent air-seeding (Sperry and Tyree 1990). It is possible that air-seeding could also occur through pores in the torus, but they are usually too small to correspond to the measured air-seeding pressures.

Why did the torus–margo membrane evolve within the gymnosperms? These gymnosperms exhibit the same wide range of vulnerability to cavitation as other plants, so the torus–margo system is not necessarily more air-tight than homogenous pits. The reason appears to be that the torus–margo membrane is about 60 times more conductive to water flow than the microporous homogenous membrane (Pittermann et al. 2005). This is a major benefit when water must cross these pits every few millimeters through the short unicellular tracheids of these species. The tracheids are particularly short in the trunks and branches of conifers and vesselless gnetophytes because they do double duty in providing mechanical strength.

7.2 Conduit Structure and Freeze–Thaw Cavitation

The link between conduit size and vulnerability to cavitation by freezing and thawing is relatively straightforward, both experimentally and theoretically. Experimentally, whether in the field or in the lab, species with wider conduits exhibit a greater loss of conductivity from freeze–thaw cycles (Hammel 1967; Cochard and Tyree 1990; Cavender-Bares 2005). In controlled centrifuge experiments, conifer tracheids and angiosperm vessels exhibit a similar relationship between conduit diameter and vulnerability (Fig. 6; Davis et al. 1999a; Pittermann and Sperry 2003). The reason that birch is more vulnerable to freezing than the fir in Fig. 3 is because it had larger diameter conduits. There is apparently nothing special about fir tracheids that make them resistant, other than their tendency to be narrow (Pittermann and Sperry 2003). Narrow angiosperm vessels are just as resistant to cavitation by freezing and thawing as narrow conifer tracheids (Fig. 6).

Theoretically, the greater vulnerability of wide conduits is explained by their predicted tendency to form larger diameter bubbles during freezing (Sperry and Robson 2001). If freezing starts at the conduit wall and moves towards the center of the lumen, air will outgas in the lumen center. The greater the cross-sectional area of the lumen, the larger the bubble diameters (D_b), and the more likely the sap P on thawing will be more negative than P^{BUB} (2) and cause cavitation and embolism. The bubbles dissolve rapidly during the thaw because the surrounding water has

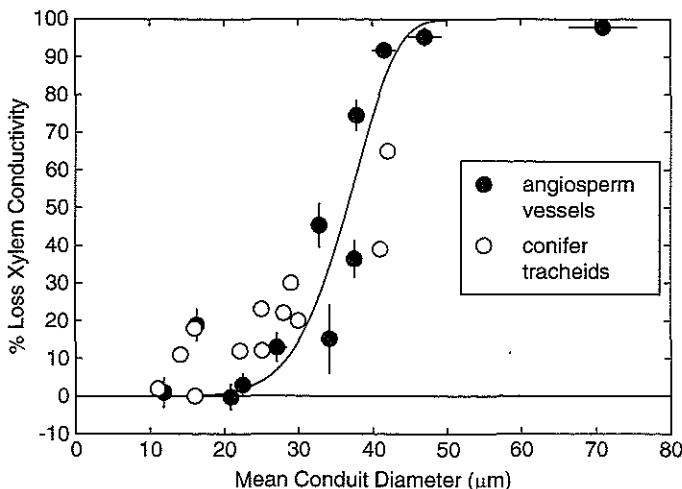


Fig. 6 Loss of hydraulic conductivity caused by a single freeze–thaw cycle at -0.5 MPa versus average conduit diameter. Data are species averages for angiosperm vessels (*open symbols*) and conifer tracheids (*closed symbols*). From Pittermann and Sperry (2003)

been degassed, so D_b is decreasing as liquid P is restored during melting (Sucoff 1969). This explains why some narrow-conduit species show no freeze–thaw effect even if exposed to very negative P (Fig. 3b): the bubbles shrink faster than negative P can be restored. It also explains the observation that more rapid thaws and also more negative P tend to increase the amount of cavitation caused by freeze–thaw cycles (Davis et al. 1999b).

Some freezing-related observations are more difficult to explain. In some species, the embolism caused by freezing increases with decreasing minimum ice temperature (Pittermann and Sperry 2006). This is not predicted by the thaw-expansion hypothesis, which depends only on the bubble size during the thaw period. A possible explanation is that the low temperature causes tissue damage which makes the vascular system more vulnerable to cavitation by water stress during the thaw (Pockman and Sperry 1997). More research is needed on this phenomenon, which can be an important factor in range limits of plants (Sect. 9.3).

8 Reversal of Cavitation

Cavitated and embolized conduits can be refilled under some circumstances. From a physical standpoint, for a conduit to be refilled, the water pressure, P , needs to be less negative than the fairly weak capillary suction the conduit lumen (diameter D_c) is capable of generating [$P^{\text{CAP}} = -4T\cos(a)/D_c$, (1)]. For a conduit of $D_c = 20$ μm , P must rise above -14.6 kPa to allow water to be pulled into the conduit by capillary action (assuming $a = 0$). The surface tension of the meniscus puts the

air under pressure, eventually dissolving away the bubble (Yang and Tyree 1992; Grace 1993). Surface sculpturing and contact angle (α) could modify the process, but little is known of such effects.

The P of the bulk xylem sap carried around the embolized conduit is rarely above the refilling threshold. Exceptions are in short plants rooted in wet soil under nontranspiring conditions (rain, night), or when P is elevated by osmotically driven root pressure (Sect. 3.3). Root pressure is particularly important in overnight refilling of herbs, and in annual spring refilling in many temperate trees and vines (Milburn and McLaughlin 1974; Sperry et al. 1987; Cochard et al. 1994; Hacke and Sauter 1996). Spring root pressures in many temperate woody species typically peak prior to leaf expansion and in a few days refill xylem conduits embolized by freeze–thaw cycles over the winter. Stem pressures generated in a few temperate trees in early spring (*Acer* species, most famously) also act to reverse winter embolism (Sperry et al. 1988).

Mysteriously, refilling has been observed in many species despite the fact that the P of the bulk xylem sap is far below the refilling threshold (Salleo et al. 1996; Tyree et al. 1999; Zwieniecki et al. 2000; Bucci et al. 2003; Stiller et al. 2005). These species apparently have a pump, no doubt powered directly or indirectly by osmosis, which delivers water to the embolized vessel at high-enough pressure to refill it. The process is metabolically dependent, because it is prevented by poisons and light starvation (Zwieniecki et al. 2000; Stiller et al. 2005). It also appears to be linked to phloem transport, because it can be inhibited by stopping phloem transport to the area by girdling (Salleo et al. 2006). The refilling has been coupled to starch hydrolysis in xylem parenchyma (Bucci et al. 2003; Salleo et al. 2009). Aside from these observations, nothing is known of how the water is pressurized and delivered to the conduit, and how it is kept pressurized in the conduit while neighboring water-filled conduits are at negative P . There are many hypotheses (Holbrook and Zwieniecki 1999; Hacke and Sperry 2003; Vesala et al. 2003), and solving the mystery is attracting much research effort.

9 Ecological and Physiological Consequences of Cavitation

Cavitation is an important factor in the adaptation of plants to their environment. Vulnerability curves reveal the physical limits to xylem pressure. Vulnerable plants like the cottonwood in Fig. 2 cannot live in the California chaparral like the hoaryleaf ceanothus because they would cavitate to death. Conversely, the ceanothus does not flourish in riparian zones presumably because it is out-competed by vulnerable species. Traits that confer tolerance to cavitation appear to come at the cost of reduced competitive ability (Sperry et al. 2006). One cost of cavitation resistance is the tendency towards narrow conduits (Fig. 5a) which reduce transport capacity. A second cost is the tendency towards dense wood tissue in arid-adapted plants that has been related to the need to reinforce the xylem conduits against

implosion under more negative pressures [Sect. 3.2; (3)]. Greater thickness-to-span ratio [t/D_c ; (3)] required to resist implosion also increases wood density (Hacke et al. 2001). Denser wood is more expensive, potentially reducing growth rates.

9.1 Stomatal Regulation

Vulnerability curves have implications for stomatal responses to both soil and atmospheric humidity. Given the large effect of friction on P (Sect. 4), the regulation of transpiration is also the regulation of P . Vulnerable species, like cottonwood, have little safety margin from cavitation (Rood et al. 2000). They require extremely good stomatal control in response to soil moisture and humidity to keep P from falling critically negative. They can also be phreatophytic, tapping into a stable water table. Such plants have been termed “isohydric” in that they maintain a nearly constant mid-day P under transpirational conditions regardless of soil or humidity (Tardieu and Davies 1993). Isohydric plants are “drought avoiders” because they prevent overly negative P by stomatal control and sometimes with reliance on ground water.

Some vulnerable plants may survive without good stomatal regulation if they live in extremely benign habitats where soil is always wet and the evaporative gradient low. Such plants are “drought susceptible” because in the absence of stomatal regulation their vulnerable xylem would quickly cavitate during soil drying and increasing evaporative gradients.

Very cavitation-resistant plants, like sagebrush or ceanothus in Fig. 2, do not require tight stomatal regulation unless soils dry out to the point where frictional gradients threaten to cause excessive cavitation. These plants typically allow their P to become more negative during drought, and have been termed “anisohydric” (Franks et al. 2007). They often do not tap into permanent ground water. Because they exhibit large negative P during droughts, they are “drought tolerators.” Despite being very resistant to cavitation, they also experience significant cavitation during drought because their pressures can become very negative (Davis et al. 2002).

9.2 Drought Responses

Plant hydraulics can inform predictions of how vegetation will respond to projected conditions of rapid climate change (McDowell et al. 2008). In areas of increased drought, drought-susceptible species should be quickly eliminated. Drought avoiders would initially do well, being protected by stomatal closure. But if droughts were long or frequent enough, chronic stomatal closure would induce physiological dormancy. In such an energy-deprived state, they would be more susceptible to pathogens, competition, and starvation. This appears to explain the massive drought-related dieback of the isohydric pinyon pine (*Pinus edulis*) in the

southwestern US (McDowell et al. 2008). Drought tolerators would initially show more cavitation than the drought avoiders, but not as much as the drought-susceptible species. Tolerators might show some dieback, but by maintaining at least some physiological activity, they would survive all but the most severe droughts. *Juniperus* species are drought tolerators (Willson and Jackson 2006). Where junipers co-occur with the afore-mentioned pinyon pine in extensive woodlands, they survive much better, although suffering more cavitation. Very severe droughts, however, will kill even junipers (West et al. 2008).

Physiological responses to environment can be quantified by the incorporation of vulnerability curves into models of the soil–plant–atmosphere continuum (Sperry et al. 1998). Such models are capable of predicting species' specific responses of plant water use to a changing environment (Jackson et al. 2000). The analysis and prediction of drought responses based on the performance of the plant's hydraulic system is receiving increased interest (Rice et al. 2004; Brodrribb and Cochard 2009).

9.3 Low Temperature Responses

Vulnerability to freezing-induced cavitation also influences plant ecophysiology. Among diffuse-porous angiosperm trees, there is a pronounced trend toward narrower conduits at higher latitude (Baas 1986). Presumably, this is adaptive in reducing the amount of winter embolism in temperate habitats. Within a given region, trees with narrower vessels tend to leaf out earlier and have longer growing seasons than trees with wider vessels, a phenology consistent with the greater resistance of narrow vessels to freeze–thaw cavitation (Wang et al. 1992). Diffuse-porous trees generally rely on multiple growth rings to supply their water, so embolism during winter would reduce growing season transport capacity, particularly in those species that do not exhibit spring refilling. Those that do rely on refilling are vulnerable to events that impair the refilling process. Large-scale dieback of paper birch (*Betula papyrifera*) in northeastern North America has been linked to winter-freezing damage of roots and the inhibition of spring root pressures for restoring transport capacity (Cox and Malcolm 1997).

Ring-porosity, which is largely a north-temperate phenomenon, may have evolved in response to the freezing problem. Ring-porous trees rely on a single growth ring for their transport, producing a ring of very large early-wood vessels to carry their water (Ellmore and Ewers 1986). These large (typically $>80\ \mu\text{m}$) vessels are exceptionally vulnerable to cavitation by freezing and thawing (Cochard and Tyree 1990). They are produced late in the spring when the risk of freezing is low, and consequently, ring-porous trees are among the last to leaf out and have the shortest growing seasons (Lopez et al. 2008). The advantage, however, is that these plants can rely on a consistent transport capacity that is less influenced by the vagaries of winter freezes and refilling mechanisms. The first freezes of fall cavitate the earlywood vessels, and they typically never function again (Sperry and Sullivan

1992). Ring-porous trees occur in the lower temperate latitudes where the frost-free period is apparently long enough for them to compete with more narrow-vesseled trees that have longer growing seasons.

In some species, for reasons that are not well understood, freezing-related cavitation is sensitive to minimum temperature (Sect. 7.2). Diploid *Larrea tridentata*, the dominant shrub of the Mojave desert in southwestern North America, becomes completely cavitared at minimum temperatures of -20°C or below. The northern limit of the Mojave diploid race corresponds closely with the -20°C minimum temperature isotherm (Pockman and Sperry 1997). The implication is that the cavitation response is an important factor limiting the northern range of the population. More research is necessary to understand why cavitation can be sensitive to the freezing temperature (Cavender-Bares 2005).

9.4 Evolutionary Responses

Vascular evolution has produced innumerable variations on the basic wick theme. Much can be learned by studying how structural modifications influence vascular function in different lineages. These “natural experiments” can be used to test a number of structure–function hypotheses.

The transition from tracheids to vessels has happened three or more times during evolution, including at least once in the flowering plants (Carlquist 1988). The classic explanation is that the multicellular vessels reduce flow resistance relative to the unicellular tracheid. Data from early-diverging angiosperm lineages contradict this explanation, however, because vessel-bearing species with “primitive” vessel morphology have similar sapwood-specific flow resistivity as their vesselless relatives. Instead, the initial advantage of vessel evolution may be the origin of separate, specialized tissues for transport, storage, and mechanical support (Sperry et al. 2007; Hudson et al. 2010). The poor hydraulic performance of primitive vessels can be attributed in part to their scalariform perforation plates. The obstructing bars of these plates are vestiges of the pitted intertracheid walls (Carlquist 1992), and they approximately double the flow resistivity of the vessel lumen. Hydraulically efficient vessels apparently evolved with the origin of obstruction-free simple perforation plates (Christman and Sperry 2010).

Vessel evolution may also have been associated with a temporary increase in vulnerability to cavitation by water stress (Sperry et al. 2007). As tracheids linked together to form long vessels, the number of pits per conduit necessarily increased, greatly increasing the probability of failure (Fig. 5b, “more pits” arrow). This trend was hypothetically compensated for by the evolution of less porous pit membrane structure (Fig. 5b, opposite the “more porous” direction).

Recent work has focused on the importance of leaf hydraulics in limiting plant productivity (Brodrribb et al. 2005). Low vein densities (vein length per leaf area) of nonflowering plants are associated with low maximum photosynthetic rates. A causal explanation is that low vein density means longer distance from the xylem

conduits to the site of evaporation (Brodribb et al. 2007). The consequently greater pressure drop is compensated for by lower diffusive conductance through stomata. The evolution of higher vein densities in later-diverging angiosperm lineages, perhaps associated with vessel evolution, may have been critical for the rise of high-productivity plants, including all major food crops (Brodribb and Feild 2010).

10 Conclusions

The science of plant water transport is equal parts of physics and biology. Plants have evolved a complex wick system that harnesses the cohesive hydrogen bond energy of liquid water and suppresses the heterogeneous nucleation of cavitation. Trade-offs between making the wick safe against failure, yet efficient in moving water, result in the process being limiting to plant performance. Failure in most cases arises from air-seeding and bubble nucleation which leads to cavitated and embolized conduits. Cavitation limits the range of negative pressures that can be harnessed to move water, and the hydraulic conductance of the wick limits the flow rate of water that can be moved at a given pressure gradient. Both limits constrain CO₂ uptake via the water-for-carbon trade-off at the stomatal interface.

The cohesion–tension mechanism has withstood numerous challenges over the years, and has considerable experimental support (summarized in Tyree 1997; Cochard et al. 2001). But there is more to be learned. Cavitation by air-seeding at interconduit pits appears to be a stochastic process that is influenced by pit quality and quantity, but the details are poorly understood. The function of the pit valves is a topic of much research because these valves are crucial to both the safety and efficiency of water transport. Other cavitation mechanisms are possible, but have not been documented. Freezing-related cavitation appears to be largely explained by the thaw-expansion mechanism, but low-temperature effects and the possibility of cavitation during the freezing phase need further research (Mayr and Sperry 2010). Perhaps the biggest mystery is how refilling can occur by an active pump that works against the negative pressure of the transpiration stream. Finally, next to nothing is known about the molecular and developmental biology underlying xylem function.

At a larger scale, the largely physical constraints on water transport translate into biological constraints on plant metabolism, growth, and survival. A quantitative grasp of plant hydraulics has considerable explanatory power. Stomatal regulation takes on new significance when viewed in the light of the limitations on the delivery of the transpiration stream (Brodribb and Holbrook 2004). Mortality events and range limits often have important links to hydraulic limitations. The productivity of plants, and how it scales with plant size, have theoretical links to vascular architecture as captured by the influential and controversial Metabolic Scaling Theory (MST; Enquist et al. 2000). The fact that the growth in the hydraulic conductance of a tree falls increasingly short of its growth in volume ultimately may play a role in limiting tree size (Ryan et al. 2006). At the ecosystem level, the physical limits

on the transpiration stream can constrain the CO₂ uptake and hence the carbon sink strength of the vegetation. The wicking of water through plant vasculature is not only a remarkable biophysical process, but it is one with far-reaching biological implications.

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