Xylem Hydraulics and the Soil–Plant–Atmosphere Continuum: Opportunities and Unresolved Issues

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ABSTRACT

Soil and xylem are similar hydraulically. An unsaturated conductivity curve for soil is called a *vulnerability curve* for xylem—but the underlying physical basis is the same. Thus, any transport model that treats unsaturated soil conductivity would benefit by also incorporating the analogous xylem vulnerability curves. This is especially the case for crop plants, which as a group have relatively vulnerable xylem. Although the cohesion–tension mechanism for xylem transport has withstood recent challenges, a number of gaps remain in our understanding of xylem hydraulics. These include the extent and mechanism of cavitation reversal and thus hysteresis in the vulnerability curve, the structural basis for differences in air entry pressure (=cavitation pressure) for different xylem types, a quantitative model of xylem conductivity, and a mechanistic understanding of how stomata regulate plant water status. Improving the representation of xylem hydraulics in models of crop water use is necessary to achieve a mechanistic link between soil water availability and canopy water use. An important additional knowledge gap concerns the hydraulics of the living tissues of absorbing roots and transpiring leaves, which are more complex than in xylem and less amenable to mechanistic modeling at present.

An understanding of the hydraulic resistances in soil and plant is fundamental to any treatment of the soil–plant–atmosphere continuum (SPAC). Without knowing these resistances and how they change with soil and plant water content, we cannot understand and predict the response of plant water use to environment. Traditionally, the treatment of soil resistances in transport models has been much more mechanistically based and complete than the corresponding description of plant hydraulics. Although complex, the physical nature of flow through soil makes it more amenable to quantitative treatment than flow through the plant. Nevertheless, plant resistance dominates the total hydraulic resistance of the continuum under moist soil conditions (Boyer, 1985; Gardner, 1965). Even under dry conditions when soil resistance increases (Jury et al., 1991), the plant resistance also increases—thus continuing to exert a major influence on water movement even during drought (Blizzard and Boyer, 1980; Nobel, 1994; Sperry et al., 1998). However, the basis for changes in plant hydraulic resistance through drought cycles has typically not been handled in a mechanistic manner in many models of the continuum.

The sophistication with which plant resistances are handled in SPAC models is improving as we learn more about the hydraulic properties of the plant vascular system. The traditional view of plant hydraulics being dominated by resistances of endodermis and root cortex (Boyer, 1985; Philip, 1966) is expanding to include well documented and surprisingly dynamic responses of xylem flow resistance to environment. The behavior of water in soil and xylem is strikingly identical, making it possible to model xylem flow with the same quantitative precision as soil flow. The result is an opportunity for SPAC models to incorporate more mechanistic and predictive treatment of plant hydraulics and a better understanding of how the SPAC is influenced by drought cycles.

Beyond this immediate opportunity, there are several unresolved issues involving xylem transport. The validity of the cohesion–tension mechanism with its seemingly counterintuitive prediction of negative water pressure comes under perennial scrutiny. Xylem cavitation and its reversal can be readily documented, but in many cases, the underlying mechanisms and linkage to xylem structure are poorly known. Quantitative models linking xylem conductivity to structure have struggled to move beyond the Hagen–Poiseuille equation, hampering the ability to quantify the role of pits and ionic effects in determining the hydraulic conductance of xylem. The stomatal response to changes in xylem and plant conductance is well characterized, but the mechanism remains unclear. Finally, although outside the main focus of this review, our understanding of the hydraulics of water transport across the living tissues of the root and leaf remains limited. Although this pathway is infinitesimally short compared with the xylem flow path, it creates significant resistance to flow, which cannot at present be modeled at the same mechanistic level as soil and xylem.

With this review, we briefly document the importance of xylem hydraulics and how it can be usefully incorporated in SPAC models before addressing the unresolved issues touched on in the preceding paragraph. A final section briefly considers analogous gaps in our knowledge of the hydraulics of nonxylary tissues of plants.

XYLEM HYDRAULICS AND SOIL–PLANT–ATMOSPHERE CONTINUUM MODELS

On a per-unit length and area basis, xylem hydraulic conductivity (volume flow rate per pressure gradient per cross-sectional area) is roughly eight orders of magnitude greater than the corresponding conductivity of root cortex and endodermis (Sperry et al., 2002b; Steudle and Peterson, 1998). This creates the impression that

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Abbreviations: cryo-SEM, freezing-stage scanning electron microscopy; SPAC, soil–plant–atmosphere continuum; Ψ, water potential.

radial flow across the root tissue is the major limiting resistance in the plant. However, when conductivity is converted to conductance (volume flow rate per pressure difference) by incorporating relative lengths and cross-sectional areas of the two tissues, the differences diminish. The xylem constitutes all but roughly 1 mm of the total length of the transpiration stream in the plant. That is 99.99% of the flow path in a 10-m tree, or 99.9% in a 1-m corn (*Zea mays* L.) plant. Furthermore, the cross-sectional area of the xylem flow path can be over four orders of magnitude less than that of the root surface area (Ewers et al., 2000). When expressed at the whole-plant level, both xylem and nonxylem conductances are of similar magnitude in well-watered plants (Tyree, 1999). An extensive literature on plant hydraulic architecture documents the variation in xylem conductivity within plants, showing that it is least in the minor stems and especially the leaves (Nardini and Pitt, 1999; Tyree and Ewers, 1991). The total frictional pressure drop in shoot xylem can exceed 1 MPa under transpirational conditions (Tyree et al., 1991). Increase in the xylem flow path with plant size is likely a major cause of the decrease in leaf-specific hydraulic conductance of plants with size (Mencuccini et al., 1997; Schafer et al., 2000; Yoder et al., 1994).

What is perhaps most important about xylem conductance is that it decreases in a predictable manner with decreasing water potential (Ψ), causing whole-plant hydraulic conductance to decrease as well (Fig. 1). The basis for the Ψ-dependent decline in xylem conductance is the same as it is for Ψ-dependent decline in soil hydraulic conductance: progressive air entry into water-filled pore space as water pressure becomes increasingly negative (Crombie et al., 1985; Jarbeau et al., 1995; Tyree and Sperry, 1989). The difference is that the pore space in the xylem is much more highly organized than in soil. There are long (millimeter to meter) and relatively wide (≈10–200 μm) tubes (the xylem conduits) to maximize hydraulic conductance coupled together with short and narrow pit connections to minimize air entry. In the inevitable event that a portion of the conduits are ruptured (xylem senescence, mechanical damage, etc.), air enters the wide conduit but tends to be stopped at the narrow pits. The structure of these interconduit pits can hold an air–water interface against a pressure difference of 1 to 10 MPa, depending on xylem type and species (Sperry et al., 1996). Nevertheless, as water pressures continue to drop, the air is eventually sucked through the pits, nucleating cavitation and embolism on a conduit-by-conduit basis. This is referred to as the *air-seeding* mechanism of cavitation (Zimmermann, 1983).

The relationship between xylem conductivity and xylem water pressure is termed a *vulnerability curve*, examples of which are shown in Fig. 1. We have intentionally shown as many crop species as possible—but data are rare for crops. Most curves are from ecophysiological studies of woody species. It is clear from Fig. 1 that crops suffer considerable cavitation within their physiological range of xylem pressure. Rice (*Oryza sativa* L.), for example, becomes more than 50% cavitated, even under well-watered conditions, and much of the drop in leaf-specific hydraulic conductance in the plant during drought can be attributed to xylem cavitation (Stiller et al., 2003). Soybean [*Glycine max* (L.) Merr.] and sugarcane (*Saccharum officinarum* L.) are similarly vulnerable. Corn also suffers considerable cavitation based on acoustic methods of cavitation detection (Tyree et al., 1986), but hydraulic data are lacking.

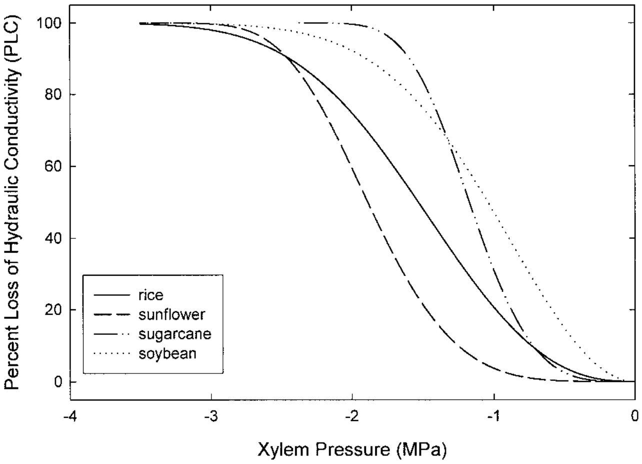

Fig. 1. Vulnerability curves of crop species, showing how the percentage loss of hydraulic conductivity in the xylem (PLC) increases as xylem pressure becomes more negative. Data from Neufeld et al. (1992), Sperry (2000), Stiller et al. (2003), and Stiller and Sperry (2002).

Models that account for variable xylem conductance have been successful in predicting the regulation of transpiration in response to soil moisture, fertilization, and soil type within species (Ewers et al., 2000; Hacke et al., 2000); the differences in water use between species and ecotypes (Kolb and Sperry, 1999a, 1999b; Sperry et al., 1998, 2002a); and in forest stands of mixed species (Williams et al., 2001, 1996). The combination of transpiration rate and soil moisture that induces complete cavitation can be predicted, allowing the assessment of safety factors from hydraulic failure. In several studies, partial or complete dieback during drought has been associated with total cavitation. This hydraulic failure usually occurs in the minor branches, which experience the lowest xylem pressures, and the smaller roots, which often have the most vulnerable xylem in the continuum (Sperry and Hacke, 2002; Davis et al., 2002; Sparks and Black, 1999).

All of these studies, however, concern woody plants under natural or seminatural conditions; the importance of cavitation for influencing herbaceous crop water use is less well characterized. In view of the close analogy between soil and xylem hydraulics, any crop SPAC model that incorporates unsaturated conductivity behavior of soil should be improved by incorporating the analogous vulnerability curve of the xylem. The two phenomena have an essentially identical physical basis and both have an important and relatively predictable effect on continuum hydraulics. For the same reason, it is important for crop physiologists to gather more data on the xylem hydraulics of crops. As irrigation water becomes even more limiting for agriculture, it will be even more important to understand crop drought sensitivity. Even in well-watered crops, cavitation may be occurring on a diurnal basis as suggested by studies on rice and corn.

UNRESOLVED ISSUES IN XYLEM HYDRAULICS

The Mechanism of Xylem Transport

The cohesion–tension theory of xylem transport comes under perennial scrutiny motivated by disbelief in the existence of negative water pressure in the xylem pore space (Canny, 1998a, 1998b). (Perhaps theories of soil water movement escape this critique because negative pressure in the soil pore space is not called a pressure but is disguised as a component of matric potential!) The most recent challenge to the theory stemmed from early attempts to measure xylem pressure with a modified cell pressure probe. Pressures below ≈ -0.3 MPa (relative to atmospheric) could not be measured, despite predictions of more negative pressure by the cohesion theory and pressure bomb measurements (Zimmermann et al., 1994). Several follow-up investigations have concluded that the probe failed to register more negative pressures because its insertion into the xylem conduit nucleated cavitation (Steudle, 2001; Wei et al., 1999a, 1999b, 2000). Within the probe's limited measurement range, negative pressures agreed with cohesion theory predictions and measurements with the pressure chamber (Wei et al., 1999b). The apparent problem with the cohesion theory now appears to be a problem with the pressure probe technique and its interpretation. Alternative theories of water movement spawned by the early pressure probe data (Canny, 1995, 1998a, 1998b) have not been substantiated (Stiller and Sperry, 1999) and suffer from internal flaws (Comstock, 1999).

The cohesion–tension theory has emerged from this rigorous re-evaluation with more experimental support than ever in its 100-plus-year history (Tyree, 1997). The added benefit of this research has been the development of new techniques for the study of xylem hydraulics. These include the xylem pressure probe, centrifugal force methods for measuring vulnerability curves (Pockman et al., 1995), freezing-stage scanning electron microscopy (cryo-SEM), and magnetic resonance imaging (MRI) methods for visually assessing embolized vs. functional xylem vessels (Canny, 1997a, 1997b; Cochard et al., 2000; Holbrook et al., 2001). In addition, the venerable pressure chamber and psychrometric methods have been successfully tested against these new techniques (Holbrook et al., 1995; Tyree, 1997).

Mechanisms of Cavitation Reversal: Vulnerability Curve Hysteresis

Just as an understanding of the hysteresis in soil moisture characteristics with drying and wetting cycles is critical to understanding soil hydraulics, so is an understanding of hysteresis in xylem vulnerability curves. If the cavitation induced by a drought cycle is permanent, hydraulic conductance in SPAC will be permanently depressed by the drought until new xylem can be produced. Based on the physics of bubble dissolution, we expect no refilling of embolized xylem conduits until the xylem pressure exceeds at the very least $P_{wv} - 2T/r$, where P_{wv} is the saturated vapor pressure, T is the surface tension of water, and r is the radius of a water vapor embolism in the conduit (≈conduit radius; Yang and Tyree, 1992). If the embolism is an air bubble, this pressure rises to $P_a - 2T/r$, where P_a is atmospheric pressure. This amounts to xylem pressure rising to within 0.1 MPa or so of P_a before the xylem sap can be pulled into the conduit and dissolve the gas bubble. In this case, we should see substantial hysteresis in the vulnerability curve (Fig. 2, expected refilling).

Many crop plants exhibit root pressure and guttation under well-watered conditions. These osmotic pressures have been implicated in the refilling of cavitated vessels in sugarcane (Neufeld et al., 1992), corn (Tyree et al., 1986), grape (*Vitis* spp.) (Sperry et al., 1987), and rice (Stiller et al., 2003), as well as several noncrop plants (Cochard et al., 1994; Hacke and Sauter, 1996; Milburn and McLaughlin, 1974; Sperry, 1993). These observations suggest a vital role of root pressure in the maintenance of hydraulic conductance and gas exchange. Without these pressures, the vulnerable xylem of crops can become permanently cavitated, with consequent reduction in gas exchange capability, even under well-watered conditions. In view of this, the phenomenon of root pressure in crops deserves more attention.

A major conundrum in xylem hydraulics is the relatively recent observation of cavitation reversal when ambient xylem pressure is *below* (more negative than) the $-2T/r$ limit. The extreme of this behavior is no hysteresis in the vulnerability curve (Fig. 2, novel refilling). While many reports of this behavior using cryo-SEM observations (Canny, 1997a, 1997b; McCully, 1995, McCully, 1999; McCully et al., 1998, 2000; Melcher et al., 2001) can be questioned based on a major artifact in the technique (Cochard et al., 2000), other observations are not so easily dismissed. Extensive experiments on the bay tree (*Laurus nobilis* L.) show rather conclusively that there can be some novel refilling (Hacke and Sperry, 2003; Salleo et al., 1996; Tyree et al., 1999). At present, there is no explanation for this behavior. It seems most likely that water is drawn into the embolized conduit from adjacent living cells by osmosis, somehow raising the water pressure above the $-2T/r$ limit while the adjacent conduits are under more negative pressure. The Ψ gradient could be generated by solute secretion into the conduit from adjacent living cells (Salleo et al., 1996; Tyree et al., 1999). Water may be prevented from leaking to the transpiration stream by air trapped in the pit chambers—allowing the air in the conduit lumen to be dissolved before the remaining pit bubbles disappear (Holbrook and Zwieniecki, 1999; Zwieniecki and Holbrook, 2000). Alternatively, if the osmoticum is impermeable to the pit membrane, it could draw water directly from the transpiration stream (Hacke and Sperry, 2003). Neither mechanism is supported by limited observations of solute content in putatively refilling conduits in bay tree (Tyree et al., 1999). Much more research is required

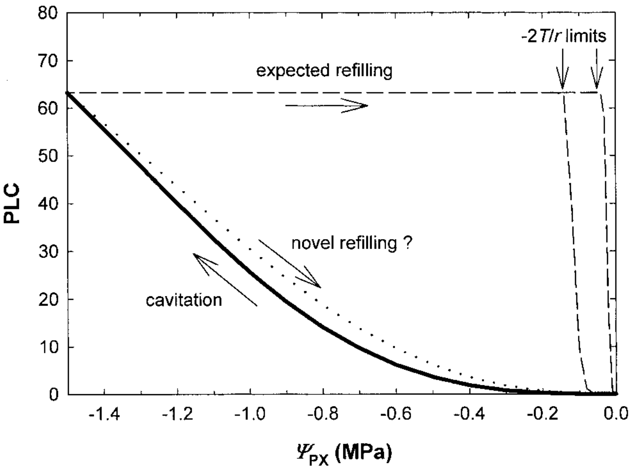

Fig. 2. Hysteresis in vulnerability curves. During dehydration, the percentage loss of hydraulic conductivity in xylem (PLC) increases because of cavitation. During rehydration, the dashed line shows the expected pattern where embolized xylem conduits are not refilled with water until the xylem pressure rises above the $-2T/r$ limit (see text), which is very close to atmospheric. The left-hand limit is for a conduit filled with water vapor, and the right-hand limit is for an air-filled conduit. The dotted line shows a novel rehydration pattern reported for some species in which refilling occurs despite substantial negative pressures in the transpiration stream. From Hacke and Sperry (2003).

to further substantiate the existence of this phenomenon, its distribution among species, the conditions for its operation, and the underlying mechanism.

The Structural Basis for the Vulnerability Curve

Understanding the structural basis for differences in cavitation resistance between species and cultivars is necessary to unravel the genetic and environmental control over this trait. A genetic basis for differences in cavitation resistance has been shown for ecotypes of sagebrush (*Artemisia tridentata*) (Kolb and Sperry, 1999a), species of *Populus* (Sparks and Black, 1999), and cultivars of sugarcane (Neufeld et al., 1992), to name a few examples. Environmental influences on cavitation resistance are most dramatically indicated by the *cavitation fatigue* phenomenon wherein a previous cavitation episode (during a drought, for example) results in a shift toward a more vulnerable xylem following the drought (Fig. 3); a shift that appears to be reversible in at least one species (Stiller and Sperry, 2002). Genetic and environmental influence over cavitation resistance must occur through modifications of xylem conduit structure because the conduit structure dictates the cavitation pressure.

The evidence for the air-seeding mechanism of cavitation is very strong. In the same way that the pressure-plate apparatus can duplicate the decline in soil water content with matric potential, the pressure-sleeve apparatus can duplicate vulnerability curves by raising the air pressure around the vascular system (Sperry et al., 1996). These experiments show that air is pushed into the vascular system at the same pressure difference known to induce cavitation, indicating that air entry is the probable cause of the cavitation. The location of the air seeding is most likely to be the interconduit pits although other sites have not been eliminated. The thin, nonlignified pit membrane is the most obvious porous region in the conduit wall, whereas other wall regions are relatively thick and heavily lignified (Fig. 4). Porosity of the pit membrane as measured directly with scanning electron microscopy (SEM) and indirectly using microbeads is consistent with the corresponding air-entry pressure in a some studies (Jarbeau et al., 1995; Sperry and Tyree, 1988). However, in other studies, the pores are either absent or much smaller than the air-seeding mechanism might suggest (Choat et al., 2003; Shane et al., 2000).

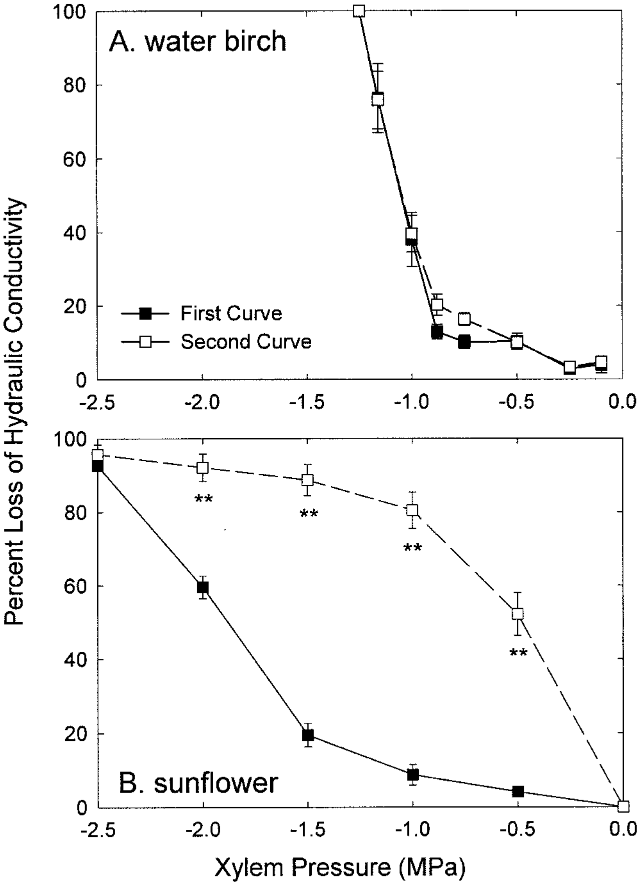

Fig. 3. The *cavitation fatigue* phenomenon. (A) Water birch (*Betula occidentalis* Hook.) stems possess the same vulnerability curve between repeated measurements on the same material (first vs. second curves). (B) Sunflower (*Helianthus annuus* L.) stems show cavitation fatigue, wherein the second curve is much more vulnerable than the first (asterisks denote significant differences at the $p <$ 0.01 level). Cavitation fatigue occurs naturally in intact, droughted plants and appears to be reversible in sunflower. From Hacke et al. (2001b).

The problem with linking pit membrane porosity to cavitation resistance is that the membrane is placed under a considerable pressure difference (typically over 1 MPa) before the air-seeding event. The membrane, unless braced by pit vestures (Zweypfennig, 1978), will be placed under stress. The displacement and stress in the membrane will depend on the elastic modulus of the membrane and the size and shape of the pit. Complicating the situation is the fact that the entire pit field

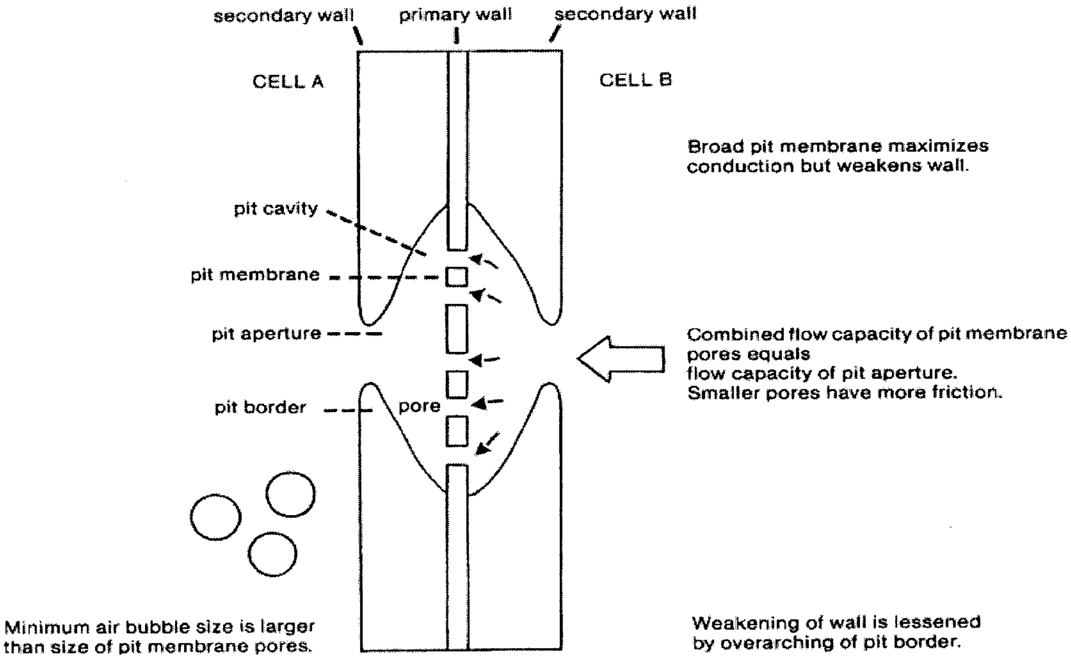

Fig. 4. Hypothetical structure–function relationships in intervessel pits. From Carlquist (1989).

of the common wall is under stress as well—not just the individual pit membrane. Air seeding will be determined by the porosity of the pit membrane under this stress—not while lying flat in its relaxed position as shown in Fig. 4. The mechanical properties of the pit membrane and its geometry are probably at least as important for determining cavitation resistance as its porosity under relaxed conditions. In fact, treatments that increase pit membrane flexibility and creep have been shown to increase vulnerability to air seeding (Sperry and Tyree, 1990).

While pit geometry is relatively easy to quantify, pit membrane mechanics are not. The elastic modulus and yield strength of pit membranes is essentially a question of primary cell wall chemistry and structure. The pit membrane is derived from the compound middle lamella of the adjacent conduits (Fig. 4) and consists of a cellulose microfibril network bound together noncovalently by cell wall matrix materials including hemicelluloses and pectins. It is possible that air seeding is actually caused by the partial rupture of these interfibrillar bonds, exposing pores that were not originally visible. This may be the basis for cavitation fatigue: A stretched pit membrane is more vulnerable to air seeding because of the weakened interfibrillar bonds (Hacke et al., 2001b). The reversal of cavitation fatigue would be achieved by the restoration of these bonds, facilitated perhaps by ingredients in the xylem sap. It is a challenge for future research to apply the growing knowledge of the physical chemistry of plant cell walls to the specific case of the pit membrane.

On a larger scale, the strength of the entire conduit wall appears to be proportional to cavitation resistance. The conduit walls must be strong enough to withstand implosion under negative pressure. Lignin mutants do in fact show collapsed xylem conduits (Piquemal et al., 1998). The greater the cavitation resistance, the lower the negative pressure can be and the stronger the conduit wall must be. Conduit wall strength, to a first approximation, is proportional to its thickness divided by the diameter of the conduit (Young, 1989). This ratio has been shown to scale tightly with cavitation resistance, causing wood density to scale with cavitation in a predictable nonlinear manner (Hacke et al., 2001a). Wall strength may actually determine cavitation resistance—in that incipient failure of a stretched wall, including its pit membranes, would open up air-seeding sites, inducing cavitation and instantly relieving the wall stress. Although pit structure has long been considered to be an optimal compromise between maximizing permeability while minimizing wall weakening (as illustrated in Fig. 4), this trade-off has never been quantified.

The Structural Basis of Xylem Hydraulic Conductance

Our understanding of how xylem structure is related to its saturated (noncavitated) hydraulic conductance is limited to the application of the Hagen–Poiseuille equation (Zimmermann, 1983). Thus, hydraulic conductivity of xylem will be proportional to the number of conduits in parallel and their diameters raised to the fourth power. While this gives a very rough relationship, the Hagen–Poiseuille conductivities generally overestimate actual values—often by more than twofold (Ewers, 1985). The discrepancy is usually explained by added resistance of flow through pits and the irregular shape and taper of the conduit lumen. There is limited evidence that if pit membranes are removed from the xylem (by cellulose digestion), actual conductivities rise to Hagen–Poiseuille values (Calkin et al., 1986). However, there has been little additional work to bolster this result, and other experiments suggest relatively little pit membrane resistance (Chiu and Ewers, 1993). Recently, physical models of conifer tracheid pit membranes have been used to predict their flow resistance, showing that they contribute ≈30% of the total xylem resistance (Lancashire and Ennos, 2002). More studies of this type are needed to obtain a general understanding of pit flow resistances. For example, although it is reasonable to hypothesize that pit membrane conductivity should scale with pit aperture conductivity (as indicated in Fig. 4), this has never been evaluated.

The importance of understanding water flow through pits is underscored by an important effect of xylem sap composition on xylem conductivity (van Ieperen et al., 2000; Zimmermann, 1978; Zwieniecki et al., 2001). Increasing the KCl concentration in the xylem sap from zero can cause a more than 2.5-fold increase in xylem conductivity in some species although a 10% increase is common. Other ions have a similar effect. According to one model, the higher ionic strength tends to shrink the pectin hydrogel of the pit membrane, opening up membrane pores and increasing their hydraulic conductivity (Zwieniecki et al., 2001). Diurnal fluctuations in xylem hydraulic conductance that are independent of temperature fluctuations (Tsuda and Tyree, 2000) may result from changes in xylem sap composition. Modulation of xylem hydraulic conductivity via sap effects on pit membrane structure may be as important as the regulation of aquaporin activity (Tyerman et al., 2002) in leaf and root cell membranes in influencing saturated plant hydraulic conductivity.

When more is learned of the structural basis of xylem conductance and cavitation resistance, we can finally begin to understand the trade-offs between the two. In soil, there is a direct relationship between the saturated hydraulic conductance and the sensitivity of soil conductivity to drying. Bigger soil pores have a higher saturated conductance but lose water more readily during a drying cycle. The same is not necessarily true for xylem because it is the pits that largely influence cavitation resistance while conductivity is influenced by the length and width of the conduit lumen. Thus, it is theoretically possible to have high hydraulic conductance and be resistant to cavitation (Tyree et al., 1994). Nevertheless, trade-offs must exist, if only at the level of the pit membrane. Only by discovering the linkage between pit structure, cavitation resistance, and hydraulic conductance can these trade-offs be characterized.

The Stomatal Response to Xylem Hydraulic Conductance and Plant Water Status

In general, there is a strong and often linear relation between the diffusive conductance of stomata to water vapor and the hydraulic conductance of SPAC. This is revealed by interspecific comparisons (Meinzer et al., 1995), intraspecific comparisons at different growth stages (Meinzer and Grantz, 1990), and intraindividual comparisons where hydraulic conductance is manipulated (Hubbard et al., 2001; Saliendra et al., 1995; Sperry et al., 1993). The experimental studies show a stomatal response within 5 min to artificial changes in hydraulic conductance. The response can be nearly exactly proportional in that a 50% reduction in hydraulic conductance induces a nearly 50% reduction in stomatal conductance, other conditions being equal.

Superficially, there is nothing mysterious about this relationship. Stomata exist to regulate plant water status via adjusting transpiration rate. Thus, stomata have a mechanism for sensing changes in plant water status and adjusting accordingly. Changing the hydraulic conductance of the continuum simply triggers a change in plant water status, which then feeds back to the appropriate adjustment in stomatal conductance. This is what makes an understanding of the hydraulic conductances in SPAC so important: Hydraulic conductance is translated by the stomatal response into adjustments in gas exchange so as to regulate plant water status. In the simplest *isohydric* plants, the stomata regulate so as to prevent Ψ from dropping below a single set point. In *anisohydric* plants, the stomata may allow a regulated drop in Ψ—conceptually via a shifting series of set points (Tardieu and Davies, 1993).

Beyond this descriptive and conceptual scenario, little is known of how the stomata sense plant Ψ, where they sense it in the plant, what chemical or hydraulic information is involved, or how the set points are controlled. While there is considerable information at the detailed level of guard cell physiology (Assmann, 1993; MacRobbie, 1997), abscisic acid action (Hartung et al., 1998; Wilkinson and Davies, 2002), and guard cell mechanics (Franks et al., 1997, 1995; Franks and Farquhar, 2001), the most basic link—the mechanism by which plant cells sense water stress—remains unknown (Luan, 2002). The stomatal response to water status is a critical area in plant physiology where there is much to learn before a mechanistic model can be achieved.

UNRESOLVED ISSUES IN EXTRA-XYLARY HYDRAULICS

In moving from soil to stomata, the transpiration stream must cross the root cortex and endodermis and move through the leaf mesophyll to the site of evaporation. These nonxylary pathways, though short in distance, have relatively low hydraulic conductivities on a length and area basis as mentioned above. Although this portion of the flow path is not the focus of this review, it is an important component of the plant's hydraulic conductance. More is known of the hydraulics of root tissue compared with the leaf mesophyll, and there are several recent summaries available (Steudle, 2000; Steudle and Heydt, 1997; Steudle and Peterson, 1998). The response of root tissue conductance in response to drought and rewatering cycles has been particularly well described in succulent species (Nobel, 1994). Suberization, cortical cell shrinkage, root–soil gaps, and root xylem cavitation all contribute to the loss of hydraulic conductance with prolonged soil drought. Hysteresis in recovery depends in part on the rate of root growth. A major developing issue in tissue hydraulics is the role of aquaporins in modulating cell membrane hydraulic conductance (Tyerman et al., 1999, 2002). Diurnal swings in root system hydraulic conductance have been linked to diurnal variation in aquaporin expression (Henzler et al., 1999). Tissue conductances may be more difficult to incorporate in general SPAC models because they lack the direct physical interaction with Ψ that is present in soil and xylem.

There is little consensus on the flow path of water in the leaf mesophyll. At issue is to what extent it is apoplastic vs. symplastic; whether the site of evaporation is near the substomatal chamber or deeper within the leaf; the extent of hydraulic contact between the different leaf tissues, in particular the epidermis vs. mesophyll; and the magnitude of the hydraulic resistance in the collective mesophyll vs. the leaf vasculature. The leaf as a whole can account for more than 50% of the shoot hydraulic resistance (Nardini and Salleo, 2000), so it is important to know how this resistance is allocated and how it varies with conditions. Cavitation within the leaf vasculature appears to be extensive and may play a role in patterns of stomatal closure within the leaf (Salleo et al., 2001, 2000) as does the degree of hydraulic contact between leaf aeroles (Mott and Buckley, 1998).

CONCLUSION

The fundamental similarity in soil and xylem hydraulics is strong rationale for incorporating both in SPAC models. The xylem of crop plants has been understudied in this regard, and there is an opportunity to improve our understanding of crop responses to water stress by characterizing their xylem characteristics. Once we learn the structural basis for key xylem traits of cavitation resistance and hydraulic conductivity, we can begin to understand their control by genes and environment. This work should focus on the structure and function of pits and their membranes, given their critical role in determining both cavitation resistance and xylem hydraulic conductivity. Although the cohesion–tension mechanism for xylem transport remains well substantiated, major challenges lie ahead in explaining novel refilling behavior of cavitated xylem and the mechanisms by which stomata regulate gas exchange in response to the hydraulic conductance of soil and plant.

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