**Perspectives
in Plant Ecology,
Evolution and
Systematics**

Functional and ecological xylem anatomy

Uwe G. Hacke* & John S. Sperry

University of Utah, Department of Biology, 257 S. 1400 E., Salt Lake City, UT 84112, USA; *corresponding author, e-mail: hacke@biology.utah.edu

Abstract

Cohesion-tension transport of water is an energetically efficient way to carry large amounts of water from the roots up to the leaves. However, the cohesion-tension mechanism places the xylem water under negative hydrostatic pressure (P_x), rendering it susceptible to cavitation. There are conflicts among the structural requirements for minimizing cavitation on the one hand *vs* maximizing efficiency of transport and construction on the other. Cavitation by freeze-thaw events is triggered by *in situ* air bubble formation and is much more likely to occur as conduit diameter increases, creating a direct conflict between conducting efficiency and sensitivity to freezing induced xylem failure. Temperate ring-porous trees and vines with wide diameter conduits tend to have a shorter growing season than conifers and diffuse-porous trees with narrow conduits. Cavitation by water stress occurs by air seeding at interconduit pit membranes. Pit membrane structure is at least partially uncoupled from conduit size, leading to a much less pronounced trade-off between conducting efficiency and cavitation by drought than by freezing. Although wider conduits are generally more susceptible to drought-induced cavitation within an organ, across organs or species this trend is very weak. Different trade-offs become apparent at the level of the pit membranes that interconnect neighbouring conduits. Increasing porosity of pit membranes should enhance conductance but also make conduits more susceptible to air seeding. Increasing the size or number of pit membranes would also enhance conductance, but may weaken the strength of the conduit wall against implosion. The need to avoid conduit collapse under negative pressure creates a significant trade-off between cavitation resistance and xylem construction cost, as revealed by relationships between conduit wall strength, wood density and cavitation pressure. Trade-offs involving cavitation resistance may explain the correlations between wood anatomy, cavitation resistance, and the physiological range of negative pressure experienced by species in their native habitats.

Key words: cavitation, drought stress, ecological wood anatomy, freezing stress, stomatal control, wood density, xylem structure

Introduction

This article describes xylem structure primarily in relation to its function in long distance water transport. Our goal is to provide a brief update of the major findings in the field of xylem structure and function since M. Zimmermann published his excellent book in 1983 (Zimmermann 1983). In the last 20 years, we have gained new insight into the phenomenon of cavitation in relation to xylem structure, effect of water uptake and transport processes on stomatal conductance and transpiration, into the hydraulic architecture of plants, and into the correlation between xylem pressure (P_x) and conduit reinforcement. This progress enables us to interpret trends in ecological wood anatomy in a more meaningful manner.

General aspects of conduit structure

Most gross features of xylem structure bear an obvious link to their function in transporting water by bulk flow under negative pressure. Mature tracheids and vessel elements are dead cell wall skeletons of pipe-like structure (Fig. 1). A protoplast is not necessary to energize or maintain the passive mode of transport, and would only impede bulk flow within and between conduits. The conduit walls are generally lignified and include a thick secondary layer. Their rigidity and strength is necessary to withstand the compression caused by negative pressure. In some situations conduit walls also function in supporting the plant body – particularly in the case of conifer stem wood. Conduit diameters span two orders of magnitude from below 5 μm in conifer needles to over 500 μm in tropical lianas. They cover an even greater range in length from a few millimetres in tracheids to over 10 m in vines and ring porous trees. Individual conduits are interconnected to form a complex continuum from the smallest roots to the ultimate veinlets of the leaves. Water flows between conduits through pit connections that consist of a porous pit membrane (derived from the primary cell walls and middle lamellae of adjacent conduits) held in a pit chamber formed by the over-arching secondary wall layer (Fig. 2). These pits function as check valves – allowing water to pass between functional conduits, yet also preventing air from leaking inside the conduit system in the event of damage. Conduits are also connected by pits to adjacent non-conduit cells.

The structure of xylem conduits bear striking contrasts to the phloem conducting cells that conduct sap under positive pressure by an active mechanism (Münch 1930; van Bel 1999). Phloem cells must remain alive to main-tain the osmotic gradient and to protect the system from leakage, but the protoplast is otherwise as empty as possible to maximize hydraulic conductance through the cell. The cell walls are thin and non-lignified as befits their need to resist tensions caused by positive pressure. The connections between conduits also function as check valves: facilitating flow between conduits, yet protecting against outward leakage upon damage (van Bel 1999).

Cohesion-tension mechanism of xylem water transport

The cohesion-tension mechanism is a passive process requiring no direct metabolic input from the plant. The necessity of a passive mechanism follows from the fact that >>90% of all the water taken up by a plant is not used directly for growth or photosynthesis, but is simply lost by transpiration as plants
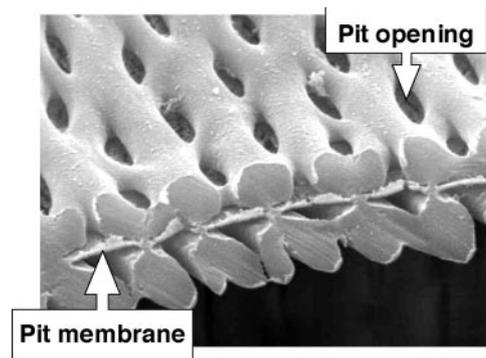

Fig. 2. SEM photograph showing the thick secondary cell wall in vessels of *Betula nigra,* and the porous pit membranes through which air-seeding nucleates drought-induced cavitation (photograph by J. Pittermann).
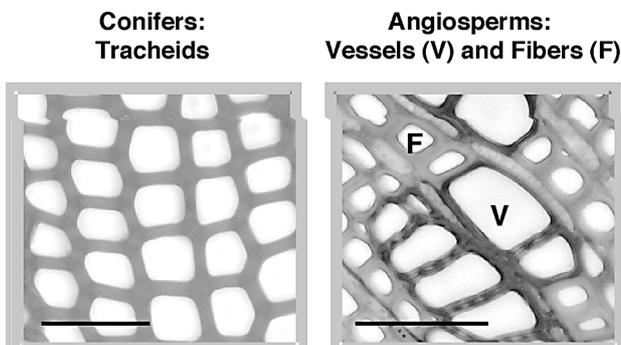
Conifers: Tracheids

Angiosperms: Vessels (V) and Fibers (F)

Fig. 1. Transverse sections of conifer *vs* angiosperm xylem. Conifer tracheids (here *Pinus nigra*) provide both transport and structural support. Angiosperm xylem (here *Acer negundo*) is more specialized. Water transport occurs in vessels (stained darker), whereas structural support is often provided by fibers. Scale bars are 50 μm.

take up CO_2 through their stomata (Kramer & Boyer 1995). If metabolic energy was directly coupled to the movement of the transpiration stream, it is probable that plants would starve to death given the typically poor ratio (e.g. 1:200–400) of the moles of carbon dioxide fixed per water transpired. According to the generally accepted cohesion theory (Böhm 1893; Dixon & Joly 1895; Zimmermann 1983; Tyree *et al.* 1994; Sperry *et al.* 1996; Tyree 1997; Cochard *et al.* 2000; Hacke 2000; Lösch 2001; Steudle 2001) water evaporates from cell walls of leaf mesophyll cells, which draws the air-water interface into the wall pores. However, capillary forces prevent the retreat of the meniscus from the pore surface, and place the water column behind the meniscus under negative hydrostatic pressure. This pulling force is transmitted to the soil water via the relatively narrow water filled channels of cell walls and the much wider channels of the xylem conduit network.

It is important to realize that the suction pressure is determined by the pore size of the cell wall channels, not the size of the xylem conduits themselves. The maximum suction pressure (ΔP) sustained by a circular air-water interface held in a pore is inversely proportional to the radius of the pore (r_p) (Tyree & Sperry 1989; Sperry 1995):

$$\Delta P = (2T \cos \alpha)/r_p \qquad \text{Eq. 1}$$

where T is the surface tension of water, and α is the contact angle between meniscus and pore wall. Even a 5 μm diameter conduit is too large to generate any significant suction (a mere 58 kPa for $\alpha = 0$), and under most conditions will be drained of its water if opened to the atmosphere. In contrast, a wetted cell wall pore of 20 nm diameter is theoretically capable of generating 14 MPa of suction. By coupling narrow cell wall pores to wide diameter xylem conduits, the plant combines the superior pressure generation of narrow pores with the superior hydraulic conductance of wide pores. According to the Hagen-Poiseuille equation, the hydraulic conductivity of cylindrical channels increases with the radius to the fourth power, and if the entire conducting system consisted of cell wall pores, their hydraulic conductance would be too low to support a plant much greater in size than a small liverwort (Nobel 1999).

In the event of damage to a conduit by herbivory, abscission of parts, storm damage or other means, air is pulled inside the damaged conduit as water is drained from it by the transpiration stream. The passage of air into adjacent intact conduits is minimized by the check-valve function of the interconduit pits, which restores a capillary barrier to the retreating air-water interface. These valves function either by capillary action at relatively small pores in the pit membrane (e.g. less than 0.1–0.2 μm diameter) as in angiosperm conduits, or in earlywood tracheids of most conifers by the aspiration of a torus against the pit aperture which provides a relatively non-porous barrier (pores <<10 nm in diameter) to the passage of air. The pores in the margo of earlywood tracheids are often too large (*c.* 0.3 μm diameter) to provide an effective seal by themselves.

Cavitation

One of the pioneers in the field of transport physiology characterized the mechanism of sap ascent like this: "Anatomically, the system is complex and the physico-chemical mechanisms at work are generally unfamiliar, because they cannot be utilized very readily in our macroscopic world; nevertheless the mechanism, in all its complexity, functions remarkable well for most of the time with an impressive, silent, efficiency" (Milburn 1996). While the mechanism does indeed work well for most of the time, Milburn (1973) was one of the first to show that it is not immune to failure. Although we calculated the theoretical suction pressure of a 20 nm diameter capillary to be 14 MPa (see above), 13.9 MPa of this pressure is in the sub-vapour pressure range and unavailable unless the plant can avoid the nucleation of the phase change to vapour (cavitation). The immediate result of cavitation is probably a vapour-filled conduit that rather quickly becomes air-filled (embolized) as gases diffuse into the void (Zimmermann 1983). As Dixon & Joly (1895) put it, "…each rupture is confined to the minute dimensions of the tracheal element in which it is formed by the fact that the woody walls, though freely pervious to water, are impervious to undissolved gas" by the check valve function described above. The direct physiological consequence of cavitation is a reduced hydraulic conductivity (Sperry *et al.* 1988a), which ultimately sets the upper limit for transpiration rate as a function of soil moisture (Sperry *et al.* 1998; Hacke *et al.* 2000a).

Cavitation is induced by freeze-thaw cycles of xylem sap and drought stress (Tyree & Sperry 1989; Sperry 1995). In the following sections, we will analyze the different mechanisms of freezing-induced *vs* drought-induced cavitation. We will identify structure-function trade-offs on the pit, conduit and tissue level, and we will evaluate some ecological implications of variations in wood structure and cavitation resistance.

Freezing-induced cavitation: the trade-off with conduit diameter and some ecological implications

When xylem sap freezes, dissolved gases come out of solution and form bubbles (Fig. 3). These bubbles can nucleate cavitation when the ice melts and the xylem water is under negative pressure (Zimmermann 1983; Sauter 1984). Whether embolism occurs as a result of freezing is in part a function of the conduit diameter and P_x (Ewers 1985; Sperry *et al.* 1994; Davis *et al.* 1999a; Lemoine *et al.* 1999; Feild & Brodribb 2001; Sperry & Robson 2001). The wider a conduit is, the bigger is the radius of the gas bubbles (r_b) that can form in it. From Eq. 1 ($\alpha = 0$), when P_x is more negative than $-2T/r_b$ (= -144 kPa/r_b (µm) at 25 °C; Ewers *et al.* 1997a), the bubble will expand and the conduit will become fully embolized (Fig. 3). Otherwise, the air in the bubble is above atmospheric pressure and can dissolve.

The trade-off between conduit diameter and the susceptibility to freezing-induced cavitation is shown in Fig. 4. Stem segments of 12 species were held at $P_x = -0.5$ MPa in the centrifuge while undergoing a controlled freeze-thaw cycle (Davis *et al.* 1999a). Whereas species with mean conduit diameters >40 µm showed almost 100% embolism after a controlled freeze-thaw cycle, species with mean diameters of <30 mm had little or no embolism. Notably, the relationship in Fig. 4 appears to hold regardless of whether the conduits are tracheids or vessels (Sperry & Robson 2001; J. Pittermann, unpubl. data). The inter-specific differences shown in Fig. 4 have implications for leaf phenology (Wang *et al.* 1992) and plant distribution (Langan *et al.* 1997; Pockman & Sperry 1997) as summarized in the following sections.

Cavitation avoidance

Conifers and angiosperms that rely on small conduits are more resistant to freezing-induced cavitation (Hammel 1967; Sperry *et al.* 1994; Davis *et al.* 1999a; Sperry & Robson 2001). Some degree of avoidance would seem to be a prerequisite for the evergreen habit of conifers in cooler regions, and for their success in high elevations and in northern regions. Although freeze-thaw events do not cause significant cavitation in the branch xylem of conifers
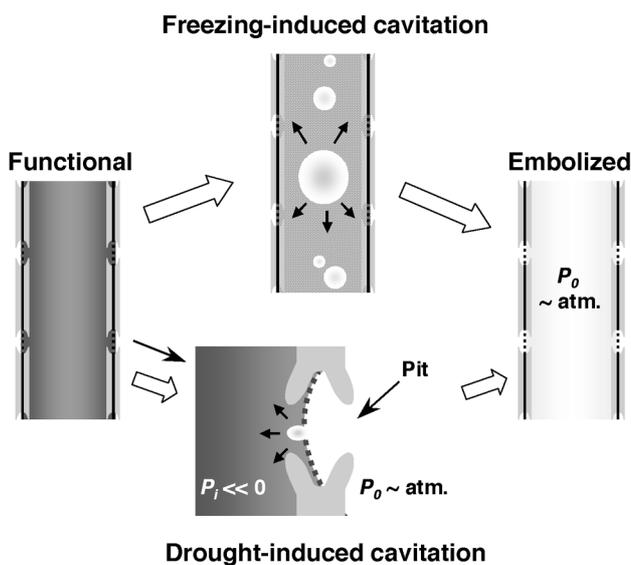
Freezing-induced cavitation

Functional

Embolized

P_0 ~ atm.

Pit

$P_i \ll 0$ P_0 ~ atm.

Drought-induced cavitation

Fig. 3. Mechanism of freezing-induced (upper panel) *vs* drought-induced (lower panel) cavitation in angiosperms. Freezing-induced bubbles may expand when the ice melts and the xylem water is under tension from transpiration. Drought-induced cavitation (air seeding) occurs when air is sucked through the largest pore of the pit membrane into a functional, water-filled vessel.
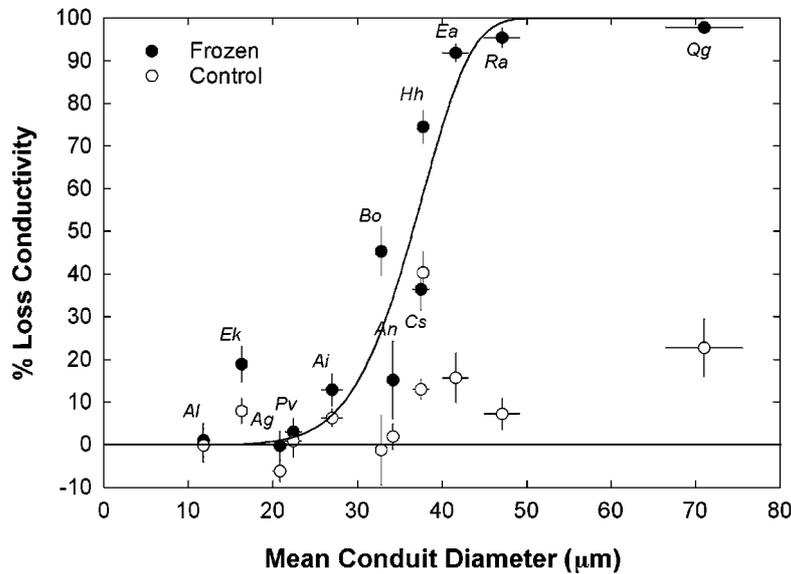
Fig. 4. Percentage loss of conductivity for frozen (●) and control (○) stems *vs* mean conduit diameter. Stems were spun in a centrifuge at a moderately negative pressure of –0.5 MPa (Al, *Abies lasiocarpa*; Ek, *Euonymus kiautschovicus*; Ag, *Acer grandidentatum*; Pv, *Prunus virginiana*; Ai, *Alnus incana*; Bo, *Betula occidentalis*; An, *Acer negundo*; Cs, *Cornus sericea*; Hh, *Hedera helix*; Ra, *Rhus aromatica*; Ea, *Eleagnus angustifolia*; Qg, *Quercus gambelii*; from Davis *et al.* 1999a).

(where tracheids are relatively narrow), conifer branch xylem does cavitate during winter (Sperry & Robson 2001). This could be caused by drought stress. When water supply is impeded by low temperature, the xylem pressure in conifers may decrease substantially (Sperry & Robson 2001). A limited water supply and low water potentials in the winter may be one reason why many conifer species show branch xylem that is more drought-resistant than what appears to be necessary from considering the water potentials in the summer (e.g. Hacke *et al.* 2000a).

Throw away strategy

In contrast, ring-porous trees (largest vessels in branches ≥100 µm; Braun 1970) and lianas lose all of their efficient earlywood vessels when the first night frosts occur (Cochard & Tyree 1990; Sperry *et al.* 1994; Hacke & Sauter 1996a; Utsumi *et al.* 1999; Tibbetts & Ewers 2000). They also must produce new earlywood vessels and leaves relatively late in spring to avoid severe cavitation from late freezes (Sperry & Sullivan 1992). As a result, ring-porous trees have a shorter growing season than diffuse-porous trees (Wang *et al.*

1992). Since ring-porous trees do not seem to refill embolized earlywood vessels (Hacke & Sauter 1996a), these vessels function for only one growing season. Consequently >95% of the flow in ring-porous *Ulmus americana* occurs in the earlywood vessels of the outermost growth ring (Ellmore & Ewers 1986). Embolized vessels in older growth rings of ring-porous trees are often sealed by tyloses (e.g. in *Quercus, Ulmus* or *Robinia*). Due to the short period over which wide vessels carry water in regions where freezing occurs, ring-porous trees do not rely on wide vessels exclusively. Their xylem also contains many smaller latewood vessels (and often tracheids) that still provide minimum flow when the network of wide conduits has failed (Cochard & Tyree 1990).

Refilling

The third strategy of coping with cavitation from freezing temperatures is to refill embolized conduits in early spring. Some trees and lianas utilize root pressure to restore hydraulic capacity in early spring before the leaf buds open (Dixon & Joly 1895; Sperry *et al.* 1987; Sperry *et al.* 1994; Hacke & Sauter

1996a; Utsumi *et al.* 1998; Zhu *et al.* 2000; Cochard *et al.* 2001). *Acer* and *Juglans* species are also known for their ability to develop positive stem pressure (Marvin & Greene 1951; Ameglio *et al.* 2001), which facilitates refilling (Sperry *et al.* 1988b; Hacke & Sauter 1996a). Apparently, some conifers are capable of refilling even when their xylem pressure is presumably substantially negative (Sperry & Robson 2001). It remains to be tested whether narrow conduits facilitate refilling.

Ecological trends

The great susceptibility of wide vessels to freezing-induced dysfunction is one reason why there is an upper limit for a useful vessel diameter in evergreen plants of cooler regions. In the evergreen flora of the California chaparral, the relatively wide-vesseled *Rhus laurina* is restricted to coastal regions whereas narrow-vesseled *Ceanothus* species extend farther inland where freezing is common. Rare freezes near the coast have been shown to completely embolize and kill back *R. laurina* shoots, whereas *Ceanothus* shoots are unaffected (Langan e*t al.* 1997; Boorse *et al.* 1998). The northern limit to *Larrea tridentata* in the Sonoran and Mojave deserts of North America corresponds with the minimum temperature isotherm found to cause 100% loss of xylem conductivity by freezing (Pockman & Sperry 1997). On a global scale, vessel diameters tend to increase with decreasing latitude, that is, in warmer regions (Baas 1986). Woodcock *et al.* (2000) found very large vessel diameters (>200 μm) and only a few narrow vessels in trees from the Amazon forest where temperatures do not fall below 0 °C. However, even in tropical regions there is an upper limit for a useful vessel diameter. The reason for this is probably that *if* a conduit becomes dysfunctional (for whatever reason), then the associated loss of hydraulic conductance will increase with increasing conduit size. A conduit of 30 μm diameter will confine an embolus to a relatively small compartment, and the loss of conductance will be minor. In contrast, the loss of a few 100 μm vessels is likely to reduce conductance significantly.

Unresolved issues

The freezing process is complex, and several issues are not fully understood. Eq. 1 predicts that freezing-induced bubbles should be big enough to cause cavitation in even the smallest conifer tracheids (Hammel 1967). It could be that the *c.* 9% increase in water volume during freezing provides a mechanism for increasing P_x during thawing (Hammel 1967). The elevated P_x could allow gas bubbles to shrink below the critical radius before P_x returns to pre-freezing values (Sperry & Robson 2001). The rate of thawing appears to be critical, because during rapid thawing, bubbles have less time to shrink and would be more likely to cause cavitation (Langan *et al.* 1997; Feild & Brodribb 2001). Another complicating factor is the potential role of xylem parenchyma cells. Pockman & Sperry (1997) found that embolism in *Larrea tridentata* increased linearly with declining temperature in the range from −11 to −20 °C. This interaction with minimum temperature is unexpected if embolism is caused just by freeze-thaw cycles. The authors hypothesized that the lower temperatures during the freeze damaged the xylem parenchyma cells, which then resulted in a greater susceptibility to water stress induced cavitation following the thaw.

Drought-induced cavitation: the trade-off with wood density and some ecological implications

The cavitation mechanism

As shown in Fig. 3, cavitation is also caused by drought stress in the absence of freezing and thawing. According to the air-seeding hypothesis (Zimmermann 1983) cavitation will occur when the ΔP between xylem water and surrounding air exceeds the capillary forces at the air-water interface – as estimated by Eq. 1. Under these conditions, air will be pulled into the conduit and the air bubble will nucleate the phase change to vapour (Fig. 3). The water pressure will rise to atmospheric, allowing the conduit to be drained by the surrounding transpiration stream. According to this hypothesis, there would be no other nucleating agent or process within the xylem that would serve to trigger cavitation independently of air seeding.

The evidence for the air seeding mechanism is substantial (summarized by Tyree *et al.* 1994 and Sperry *et al.* 1996). The largest pores in conduit walls appear to be in inter-conduit pit membranes, and these are the

supposed sites of air seeding (Sperry *et al.* 1996). Using micro-beads of defined diameters, Jarbeau *et al.* (1995) found a good correspondence between cavitation resistance and pit membrane porosity in selected chaparral species (see also Shane *et al.* 2000).

It is important to realize that the size of pit membrane pores that cause air seeding is probably related to the mechanical properties of the membrane. The pores in a 'relaxed' pit membrane may be considerably smaller than the ones in a stretched membrane where air seeding is actually occurring. This may explain why SEM studies or micro-bead perfusions that concern pit membranes in the relaxed state can find pore sizes that are too small to explain air seeding according to Eq. 1 (Choat *et al.* 2000). As a result, in order to relate cavitation resistance to pit properties, we should also account for the strength and elasticity of pit membranes as well as the geometry of the entire pit complex. Information about the pore size in a stretched membrane is more meaningful than data on pore sizes of a relaxed membrane.

Consistent with structural differences in their pitting, conifers show a different form of air seeding than angiosperms. In conifer tracheids, pores in the margo are usually too large to contain an embolus. Spreading of an embolus in conifers is prevented by the torus (a thickened region of the membrane), which blocks the pit opening (Zimmermann 1983). Air seeding probably occurs when the torus is ripped out of its sealing position at the overarching pit border (Sperry & Tyree 1990). Drought-induced cavitation in conifers is thus a function of the pressure difference across the pit membrane, the elasticity and mechanical strength of the membrane and of pit geometry.

The trade-off with wood density

Cavitation resistance is generally well adjusted to the range of P_x that plants experience in their natural habitat (Sperry 1995; Brodribb & Hill 1999; Davis *et al.* 1999b; Hacke *et al.* 2000b; Pockman & Sperry 2000; but see Pinol & Sala 2000). In Fig. 5, cavitation resistance of roots and stems of seven desert shrubs is plotted *vs* the average annual minimum (most negative) P_x from three growing seasons. The variation in minimum P_x was
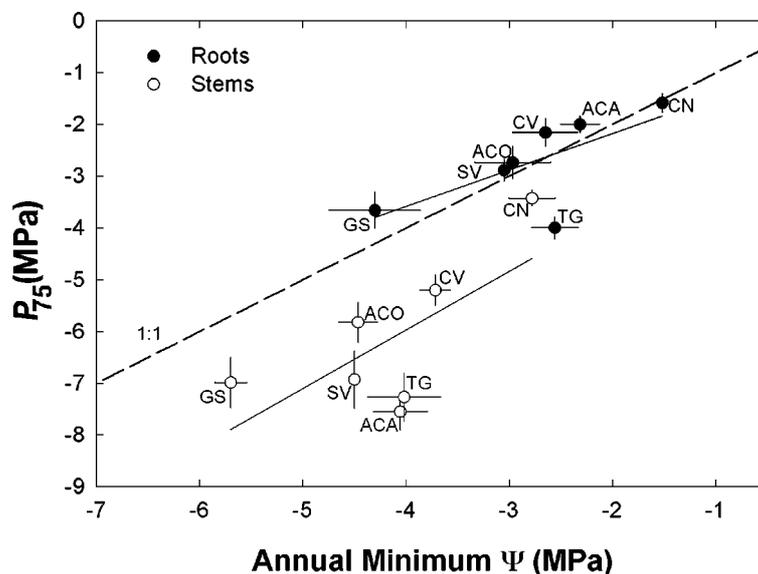

Fig. 5. The resistance to drought-induced cavitation (expressed as the xylem pressure inducing 75% loss of hydraulic conductivity, P_{75}) as a function of the average minimum xylem pressure (predawn xylem pressure for roots, midday xylem pressure for stems) from three growing seasons in Great Basin shrubs. Roots were more susceptible to cavitation than stems and were predicted to suffer more cavitation *in situ* (ACA, *Atriplex canescens;* ACO, *Atriplex confertifolia;* CN, *Chrysothamnus nauseosus;* CV, *Chrysothamnus viscidiflorus;* GS, *Grayia spinosa;* SV, *Sarcobatus vermiculatus;* TG, *Tetradymia glabrata*; J. S. Sperry & U. G. Hacke, unpubl. data).

a function of different rooting depths between these co-occurring species rather than different habitats (J. S. Sperry & U. G. Hacke, unpubl. data). Cavitation resistance is expressed as the P_x inducing 75% loss of hydraulic conductivity (P_{75}); this value was chosen over the previously used P_{50} (e.g. Hacke *et al.* 2000b) because it better indicated the variation in cavitation resistance in desert plants where the beginning of the vulnerability curve can be altered by exposure to cavitating pressures *in situ* (Pockman & Sperry 2000; Hacke *et al.* 2001a). Generally, the lower the minimum P_x was, the lower was the P_{75}. Roots were more susceptible than stems (less negative P_{75}'s). Moreover, the graph reveals that most root data points were near or above the 1:1 line, whereas stems were well under the 1:1 line. This predicts that roots experienced more cavitation than stems. We have found this pattern in many woody plants. Roots, particularly small roots, can be the Achilles heel for water transport under drought conditions. We will return to this subject in a later section.

The relationship between minimum P_x and cavitation resistance shown in Fig. 5 (see also Pockman & Sperry 2000) indicates that there has been selective pressure for developing xylem that is resistant enough for the operable pressure range of a species, but not overly resistant. This indicates that there is a cost in-

volved in developing drought-resistant xylem. We saw that there is a clear trade-off between conduit diameter and the susceptibility to freezing-induced cavitation (Fig. 4). However, this relationship is ambiguous with regards to drought-induced cavitation. Figure 6 shows that there was a rather weak relationship between the P_x inducing 50% loss of hydraulic conductivity (P_{50}) and conduit diameter in conifers, and no relationship at all in angiosperms. This is not surprising given the fact that drought-induced cavitation depends on pit membrane properties, which are at least partially uncoupled from conduit diameter.

Recently, Hacke *et al.* (2001b) presented evidence for a trade-off between the resistance to drought-induced cavitation and construction cost, specifically wood density (D_t). In a survey with 48 angiosperm and conifer species from 16 families (Table 1), the authors found that greater D_t was associated with more negative P_{50} within the angiosperm and conifer groupings (Fig. 7). The densest wood did not occur in the tallest trees or plants from the timberline that are struggling with wind and ice loads. The densest conifer xylem was from low elevation arid-adapted species like *Juniperus osteosperma* and *Pinus edulis* rather than the high elevation mesic-adapted ones like *Abies lasiocarpa* or *Pinus flexilis*.
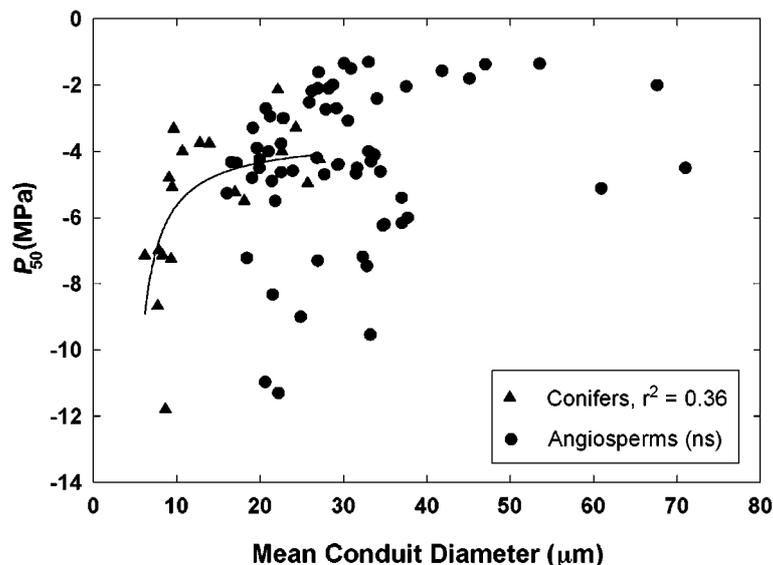

Fig. 6. The xylem pressure inducing 50% loss of hydraulic conductivity (P_{50}) *vs* mean conduit diameter in conifers (triangles) and angiosperms (circles). Species are given in Table 1. Same species as in Figs. 7, 8, & 10 (Hacke *et al.* 2001b). There was no correlation in the angiosperm data set.

Table 1. List of species used in Figs 6, 7, 8 and 10; alphabetic by family.

Conifers	Angiosperms	
Cupressaceae	Aceraceae	Hippocastanaceae
Juniperus monosperma	*Acer grandidentatum*	*Aesculus hippocastanum*
Juniperus osteosperma	*Acer negundo*	
Juniperus scopulorum	*Acer rubrum*	Oleaceae
		Fraxinus velutina
Pinaceae	Anacardiaceae	
Pinus edulis	*Rhus laurina*	Rhamnaceae
Pinus flexilis		*Ceanothus crassifolius*
Pinus monophylla	Asteraceae	*Ceanothus cuneatus*
Pinus nigra	*Artemisia tridentata* ssp. *tridentata*	*Ceanothus leucodermis*
Pinus ponderosa	*Artemisia tridentata* ssp. *vaseyana*	*Ceanothus megacarpus*
Pinus taeda	*Artemisia tridentata* ssp. *wyomingensis*	*Ceanothus oliganthus*
Pseudotsuga menziesii	*Baccharis salicifolia*	*Ceanothus spinosus*
	Baccharis sarothroides	
	Chrysothamnus nauseosus	Rosaceae
	Chrysothamnus viscidiflorus	*Adenostoma fasciculatum*
		Prunus virginiana
	Betulaceae	
	Alnus incana	Salicaceae
	Betula nigra	*Populus angustifolia*
	Betula occidentalis	*Populus fremontii*
		Populus tremuloides
	Fabaceae	*Salix goodingii*
	Acacia constricta	
	Acacia greggii	Tamaricaceae
	Cercidium microphyllum	*Tamarix ramosissima*
	Prosopis velutina	
		Tiliaceae
	Fagaceae	*Tilia cordata*
	Quercus gambelii	
		Zygophyllaceae
	Fouquieriaceae	*Larrea tridentata*
	Fouquieria splendens	

Maximum densities in angiosperms were not in tall trees, but in diminutive desert shrubs. As examined in the following section, stronger wood may be required to contain the much more negative xylem pressures in the conduits of cavition-resistant species.

From an ecological perspective, the D_t vs P_{50} relationship shown in Fig. 7 suggests an important cost to the plant of transporting water under negative pressure. High D_t represents higher construction costs, reduced growth rate, and lower storage capacity. Conifers have the advantage over angiosperms in that they can achieve a given P_{50} at less cost. This must compensate to some extent for the lower maximum conducting efficiency of tracheid-based xylem, and correspondingly lower gas exchange and photosynthetic capacities in conifers. When low resource availability prevents high gas exchange and photosynthetic rates across all life forms, the cheaper conifer xylem may confer a competitive advantage. This may contribute to the rapid expansion of drought-resistant *Juniperus* species into arid shrub and rangelands across the western USA once fire frequency is reduced (West 1989). It may also contribute to the success of conifers in achieving massive height and great longevity. It is probably not accidental that the tallest, and also the oldest trees on earth (*Pinus aristata* trees can get >4000 years old) are conifers. Apparently their relatively simple xylem structure is well adjusted to a long-term growth strategy as well as resistance to freezing-induced cavitation and success in cold environments.

The relationship between P_{50} and D_t was not a consequence of a more fundamental relationship between P_{50} and conduit diameter. Plotting diameter vs D_t gave a significant but
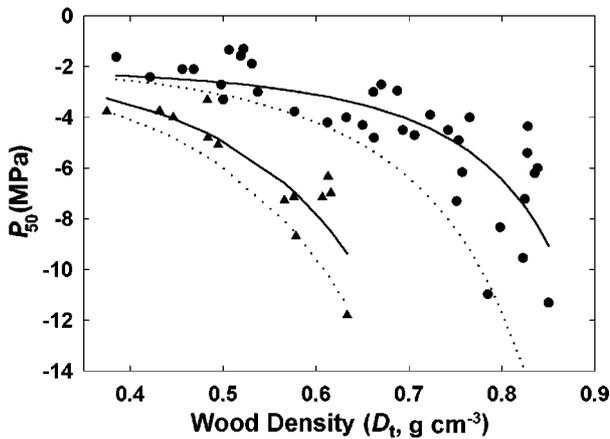
Fig. 7. P_{50} vs wood density for angiosperm (circles) and conifer stems (triangles). Same species as Figs. 6, 8, 10. Drought-resistant xylem showed greater density in both conifers and angiosperms. Conifers achieve a given P_{50} with less biomass (lower density) than angiosperms. Solid curves represent expected trend based on conduit reinforcement against implosion by negative pressure; the r^2 of the curve fit was 0.62 in angiosperms and 0.73 in conifers. Dashed curves suggest a lower boundary line set by a conduit implosion limit (from Hacke *et al.* 2001b).

weak relationship for conifer stems, and no relationship for angiosperm stems at all (Fig. 8). The lack of a correlation between D_t and diameter in angiosperms is in part because D_t is influenced by the presence of fibers in angiosperm wood (Fig. 1).

Conduit reinforcement and the risk of implosion

Hacke *et al.* (2001b) examined the variation of D_t shown in Fig. 7 from the perspective of supporting the xylem pipeline against implosion by negative pressure. It has been recognized for a long time that conduits carrying water under negative P_x need reinforced and lignified cell walls to prevent implosion. However, to our knowledge this has never been tested in a quantitative manner, nor has conduit rein-

forcement ever been related with the actual pressure range that conduits experience.

Large bending stresses can arise in the double wall between water- and gas-filled (embolized) conduits (Fig. 9). The conduit walls must be strong enough to withstand such stress. The thicker the double wall (t in Fig. 9) relative to its maximum span (b), the greater the reinforcement against bending. Hacke *et al.* (2001b) used the P_{50} as a proxy for the minimum water pressure in a species (P_i in Fig. 9). The lower the P_{50}, the thicker must the wall be relative to its span to maintain structural integrity. Standard engineering equations predict the following relationship:

$$P_{50} = -C/k\,(t/b)_h^2 + P_o \qquad \text{Eq. 2}$$

where C is a constant that includes the failure stress of the wall material, k is the safety fac-
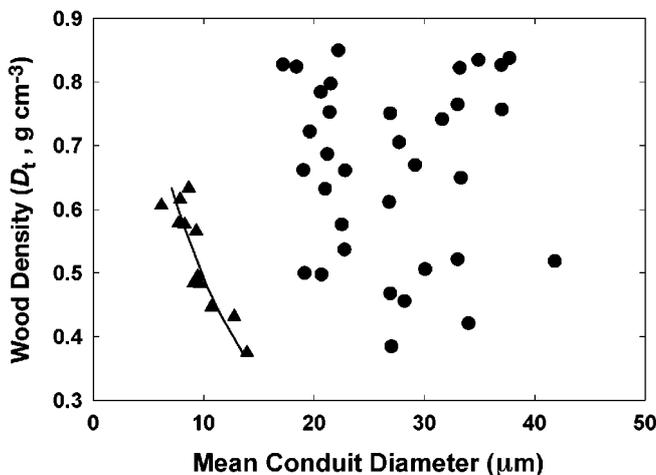

Fig. 8. Wood density *vs* mean conduit diameter in conifers (triangles) and angiosperms (circles). Same species as in Figs 6, 7, 10. The relationship was significant in conifers. There was no correlation within angiosperms partly due to the presence of fibers.
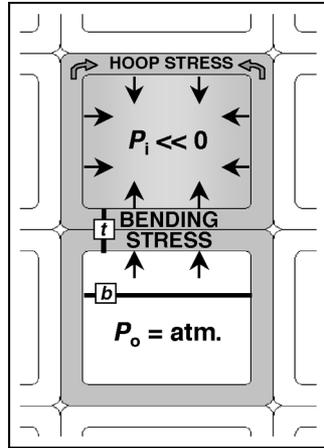
Fig. 9. Stresses in the conduit wall from negative pressure (P_i) in a water-filled conduit (shaded). Bending stresses occur in the common wall between an embolized and water-filled conduit. Bending stresses are related to the thickness of the double wall (t), its span (b), and the pressure difference $P_i–P_o$, where P_o is the gas pressure in the embolized conduit (from Hacke *et al.* 2001b).

tor from failure, and P_o is the gas pressure in an embolized conduit. The $(t/b)_h{}^2$ equals $(t/b)^2$ for conduits of the hydraulic mean diameter for the sample.

The $(t/b)_h{}^2$ within angiosperm and conifer species was directly proportional to cavitation resistance as predicted from Eq. 2 for a constant k within each group (Fig. 10). The dotted 'implosion' line in Fig. 10 represents $k = 1$; the less steep slopes of the data indicate a $k > 1$ for angiosperm and conifer species. Although our estimates of the relative safety factors between conifers and angiosperms will probably change as we learn more about the effect of pit structure on wall strength (not accounted for in Eq. 2 or Fig. 10), it appears that conifers have a higher safety factor from implosion than angiosperms. This is in agreement with the double role of conifer tracheids in providing both transport and structural support for the plant. Vessels are specialized in transport, and mechanical support of the plant in angiosperms is mainly provided by the fiber matrix.

The fact that conduit dimensions t and b scale with the risk of implosion helps explain the D_t vs P_{50} relationship in Fig. 7. The D_t is a function of (t/b). Substituting this function into Eq. 2 provides an estimate of the D_t vs P_{50} relationship. These estimates are represented by the curved lines in Fig. 7 which explain 62% of the variation in angiosperms and 73% in conifers. The dashed curves in Fig. 7 suggest a lower limit on the relationship set by
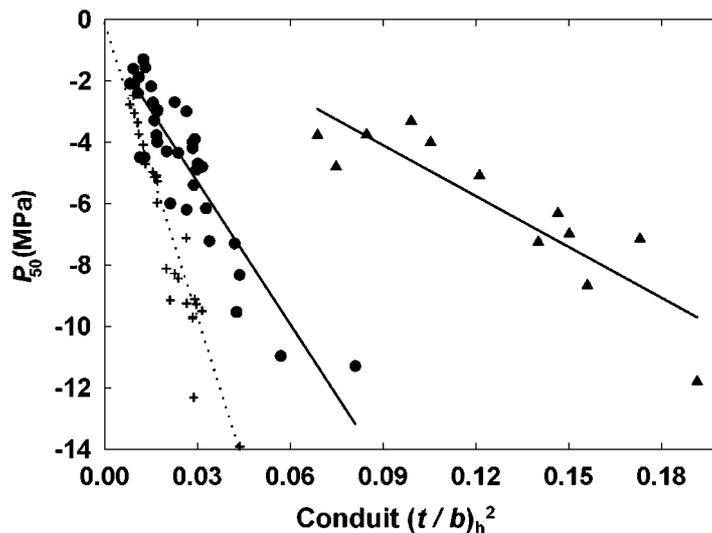

Fig. 10. P_{50} vs wall strength (expressed as $(t/b)^2$) for vessels in angiosperm stems (circles, $r^2 = 0.81$) and tracheids in conifer stems (triangles, $r^2 = 0.78$). Same species as in Figs. 6–8. The dashed line shows the estimated implosion limit for angiosperms and conifers ($r^2 = 0.98$, data extend off scale). Vessels showed a lower estimated safety margin from implosion than tracheids (from Hacke *et al.* 2001b).

conduit implosion: there can be no wood that is both light and also resistant to cavitation.

The strong relationship in Fig. 10 indicates that conduit $(t/b)^2$ can be an excellent structural correlate with P_{50} – much better than conduit diameter alone (plotted for the same species in Fig. 8) or wall thickness alone. With the $(t/b)^2$ ratio, or more refined structural indicators of wall strength, we may even be able to predict cavitation resistance from anatomy with fair precision.

Implications for gas exchange

The resistance to drought-induced cavitation has important implications for the stomatal control of transpiration and water use. Gas exchange will lead to desiccation and death if the water supply line is interrupted by cavitation. The xylem pressure causing 100% cavitation in the xylem (P_{100}) places an absolute lower limit on the plant water status that permits sustainable gas exchange. This is also the limit to the lowest soil water potential from which the plant can extract water (analogous to the 'permanent wilting point'). In the cases where P_{100} is less negative in root than shoot xylem, it is the root P_{100} that proves to be limiting under soil drought conditions (Kolb & Sperry 1999; Hacke *et al.* 2000b). Where there is an insufficient amount of absorbing root area relative to transpiring shoot area, there can also be a critical loss of hydraulic conductivity in the soil before P_{100} is reached in the plant, leading to an even greater restriction on gas exchange. A variety of theoretical and empirical studies have shown that one of the major adaptive 'reasons' for stomatal regulation in response to water stress is the avoidance of these hydraulic limitations. Stomata function in regulating plant water status, and therefore are necessarily responsive to changes in hydraulic conductance. As a result of this feedback, changes in hydraulic conductance have a significant (albeit indirect) influence over plant water use. Readers interested in this field are referred to Sperry *et al.* (1998), Hacke *et al.* (2000a), Nardini & Salleo (2000) and Sperry *et al.* (in press).

The role of matrix cells in water transport

Across different plant families, there is a great variety of the cell types bordering on a vessel and forming a matrix around the conducting network (Braun 1970). What is the functional significance of these matrix cells in terms of water transport? – A vessel can be in a group with other vessels. This is often observed in riparian *Betula, Alnus, Acer, Liquidambar* or *Carpinus* species. This trait is suggestive of great conducting efficiency, because it indicates that vessels overlap for long distances. For the same reason, this trait may also offer less effective cavitation containment.

Vessels are often adjacent to tracheids, for instance in *Quercus* and xeric *Ceanothus* species. Water-filled tracheids may act as a shield around vessels, protecting them from air entry. Vessels can be embedded in a matrix of dead and/or living fibers or can be adjacent to ray parenchyma or 'contact cells'. Contact cells are specialized in the exchange of solutes with vessels. In sugar maple they are anatomically distinguished by having numerous large pits, which face the vessels like windows (Sauter *et al.* 1973). Contact cells show a high enzyme activity, which is related to the release of solutes into the xylem sap in early spring. The release of sugar into the xylem sap before budbreak facilitates 'water shifting' (Braun 1984) and positive xylem pressure in some trees. It remains to be tested whether contact cells play an active role in embolism reversal although there is some indirect evidence for this (Salleo *et al.* 1996; Zwieniecki & Holbrook 1998; Tyree *et al.* 1999).

From the perspective of xylem biomechanics and long-distance water transport, it is noteworthy that the reinforcement of the fiber matrix is linked to the magnitude of negative pressure in the conduit system (Hacke *et al.* 2001b). Xeric plants with low P_{50}'s do not only show thick conduit walls, but usually also thick fiber walls. This is very obvious in *Larrea tridentata*, xeric Chenopodiaceae or xeric *Ceanothus* species. A dense fiber matrix may play a supporting role for vessels carrying water under substantially low pressure. Fiber density may be directly related to protecting the vessels from collapse, if, for example, fibers must bear some of the stresses propagating from the vessel walls. A dense fiber network could also compensate for the areas of considerable weakness in the wood, which are caused by large vessel luminae or large clusters of vessels (F.W. Ewers, pers. comm.).

Hydraulic architecture and vessel length

Trees show a consistent decline in their leaf specific xylem conductivity as water moves from trunk to minor branches and leaves (Zimmermann 1978). This results in ever steeper pressure gradients and lower P_x towards the distal ends of the flow path. According to the 'segmentation hypothesis' (Zimmermann 1983) this could be adaptive by insuring that cavitation would be confined to 'cheap' distal organs that could be sacrificed during a drought. The designed loss of leaves and small branches would relieve xylem tension in more basal parts of the plant, and would therefore contribute to their survival under water stress.

The segmentation hypothesis has been supported in a few well-documented cases. It was first demonstrated in the palm *Rhapis excelsa*, where drought-induced embolism was preferentially confined to petioles (Sperry 1986). Evidence for designed failure in petioles and small branches has been found in walnut (Tyree *et al.* 1993), and *Populus* species growing along river valley floodplains (Rood *et al.* 2000). Rood *et al.* (2000) proposed that the great vulnerability to cavitation of riparian cottonwoods is a component of an unusual drought adaptation. They argued that under water stress cavitation proceeds in a non-uniform manner throughout the shoot. This would be due to variations in P_x and cavitation resistance of individual branches, and it would explain the patchwork appearance in which some branches senesce and die while others remain green and survive.

Recent studies have shown that cavitation resistance varies not only among branches, but usually even more so between roots and branches. Roots, particularly small roots, are often more susceptible to drought-induced cavitation than branches (Fig. 5; Sperry & Saliendra 1994; Alder *et al.* 1996; Hacke & Sauter 1996b; Mencuccini & Comstock 1997; Kolb & Sperry 1999; Hacke *et al.* 2000a, b). As mentioned above, hydraulic failure under drought conditions can be triggered by cavitation in roots (Kolb & Sperry 1999; Hacke *et al.* 2000a). There can also be differences in cavitation resistance within a root system, and these differences have implications for various aspects of plant water relations. Hacke *et al.* (2000b) found that taproots of the deep-rooted Great Basin shrub *Chrysothamnus nauseosus* are considerably more resistant to cavitation than small roots. This would allow water transport from deeper soil layers where water status is more favourable, even when the more susceptible small roots in shallow and dry soil layers have become heavily embolized. Zimmermann's segmentation concept, which originally applied for aboveground xylem, may be even more applicable and relevant to the root system. This view is supported by results of North *et al.* (1992) who found that designed cavitation in junctions between lateral and major roots of desert succulents plays an important role in hydraulically isolating the plant from the drying soil. Differences in cavitation resistance among roots could also affect the potential for hydraulic lift.

While most work on plant hydraulic architecture has had a strong empirical and descriptive basis, recently it has been addressed from a very different theoretical perspective. The model of West *et al.* (1997) predicts how fluid transport in both plants and animals constrains their metabolism. Their analysis suggests that transport constraints underlie the ubiquitous quarter-power scaling laws in biology. However, their representation of the plant vascular system and branching system is too unrealistic to inspire confidence. The vascular system is represented as a strict pipe model with single vessels of equal diameter running the length of the plant such that the total number of vessels at any point is equal, as are their diameters and areas. Later versions have allowed for more realistic tapering to the vessels, but otherwise still keeping to the unrealistic pipe model (Enquist *et al.* 2000). The representation of branching structure is unrealistic for several reasons, one being no provision for apical dominance. Nevertheless, the broad theoretical perspective of this work is refreshing and exciting, and it will no doubt inspire more anatomically correct models in the future.

Vessel length distribution in plants

Hydraulic segmentation will be reflected in an appropriate vessel length distribution throughout the plant. Vessel length is positively correlated with vessel diameter (Zimmermann & Potter 1982; Ewers & Fisher 1989; Kolb & Sperry 1999). Ring-porous trees with wide earlywood vessels ($\geq$100 µm diameter) and grapevine have maximum vessel lengths of many metres. The vessels of diffuse-porous

trees and shrubs are much narrower and are usually well under one metre in length (Zimmermann 1983; Ewers & Fisher 1989; Sperry *et al.* 1994; Hacke & Sauter 1995; Kolb & Sperry 1999). The major roots do not only show wider (Sperry & Saliendra 1994; Alder *et al.* 1996; Hacke *et al.* 2000b), but usually also longer vessels than shoots (Zimmermann & Potter 1982; Kolb & Sperry 1999; but see Ewers *et al.* 1997b).

Frequency histograms show that length profiles are usually skewed toward shorter conduits (e.g. Zimmermann & Jeje 1981). The safety *vs* efficiency dilemma also sets upper limits on vessel length. If we assume that pit membrane resistance represents a major component of the total resistance to flow (which we do not know yet, Calkin *et al.* 1986; Chiu & Ewers 1993), then the evolution of vessels should move toward long conduits that offer little hydraulic resistance. However, consider the extreme situation where a single set of conduits traverse the entire flow path in a plant. If 50% of the conduits become dysfunctional at one point in the flow path (due to drought stress, a breaking branch or dying roots for instance), then the whole-plant conductance would be reduced by 50%. In contrast, if the flow path consists of ten conduit lengths, then the same point injury of 50% would cause less than 9% loss of whole-plant conductance (Comstock & Sperry 2000). This is because hydraulic resistances are additive in series.

The analysis of Comstock & Sperry (2000) showed that shorter conduits and a greater containment of cavitation allow lower leaf xylem pressure and higher flow rates than in a plant with insufficient cavitation containment. When flow rate is maximized and leaf xylem pressure is minimized in this scenario, cavitation would be confined to distal branches and petioles. This would protect the integrity of the basal axes, and would thereby maintain a sufficient whole-plant conductance. It follows that vessels should be particularly short in these distal organs that are experiencing the lowest xylem pressure. In the interest of higher conductance, vessels can be longer in basal portions of the flow path where cavitation is rare due to less negative xylem. Where it has been measured, vessel length in petioles can indeed be much shorter than in main branches (Salleo *et al.* 1985; Hacke & Sauter 1996b). It should be noted that the situation in a real plant is more complex than in the model of Comstock & Sperry (2000), because different plant organs often show different resistances to cavitation. The great susceptibility of small roots to cavitation and their high turnover rate suggest that vessels in these peripheral organs should be short, so that emboli cannot spread into larger transporting roots.

Interconduit pits: potential structure-function trade-offs and dynamic changes in pit membrane permeability

We already saw that in both angiosperms and conifers pit structure is crucial for determining the resistance to drought-induced cavitation. Several structure-function trade-offs should become apparent at the pit level. First, there should be a clear safety *vs* efficiency trade-off at the pit level. On the one hand, large pores in pit membranes will facilitate flow. On the other hand, large pores will compromise cavitation containment, at least in angiosperms, and will allow the spreading of embolism even at moderately negative P_x (Eq. 1). Second, there could be a trade-off between conducting efficiency and wall strength. Larger and more frequent pit membranes will facilitate transport, but may require thicker secondary cell walls to compensate for a potential weakening of wall strength. Wider pit openings, i.e. less overarching of the secondary cell wall, would probably increase flow rates, but may also increase the risk of conduit implosion due to negative water pressure inside the conduit (Hacke *et al.* 2001b). The importance of these trade-offs remains to be investigated, because of the great difficulty in quantifying flow resistance of pits.

Recent findings highlight the importance of pit membranes in determining flow rates in the xylem and in dynamically altering cavitation resistance. Van Ieperen (2000) and Zwieniecki *et al.* (2001) found changes in hydraulic conductivity in response to solution ion concentration and pH. The effect was localized to pit membranes. Zwieniecki *et al.* (2001) suggested that microchannels in the pit membranes were altered by the swelling and deswelling of pectins, which may act as hydrogels.

Recently, Hacke *et al.* (2001a) tested cavitation resistance before and after a controlled cavitation-refilling cycle. Most species showed a 'cavitation fatigue', i.e. a considerable re-
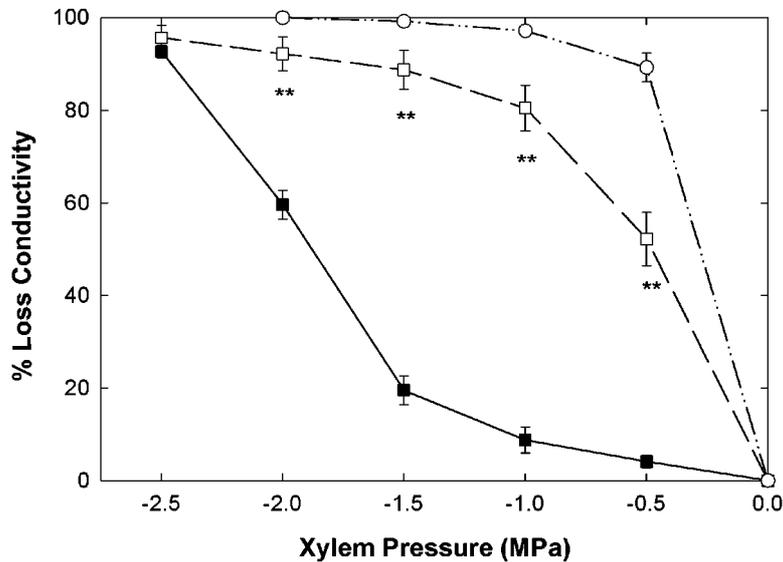
Fig. 11. Native (■) *vs* stressed (open symbols) vulnerability curves showing the 'cavitation fatigue' phenomenon in *Helianthus annuus*. Stressed stems were refilled in the laboratory. Water stress was either induced by centrifuging (□) or by air-drying of intact plants (○). The fatigue response was independent of how water stress was induced, but proportional to the amount of cavitation during stress (from Hacke *et al.* 2001a).

duction in cavitation resistance after a cavitation-refilling cycle (Fig. 11). Observations from *Helianthus annuus* showed that cavitation fatigue was proportional to the level of water stress plants had experienced: plants that had experienced severe drought were particularly susceptible to re-cavitation. This is apparently responsible for the large amount of highly vulnerable xylem found in desert plants and other species that are commonly exposed to cavitation *in situ* (Pockman & Sperry 2000; Hacke *et al.* 2000b). Interestingly, the cavitation fatigue in sunflower is reversed following a drought in association with the natural refilling of the embolized conduits. Components of the native xylem sap appeared to be essential for the fatigue repair (V. Stiller & J.S. Sperry, unpubl. data). The implication is that there is much to be learned about the physical chemistry and biomechanics of interconduit pits.

Conclusion and perspective

In the last 20 years, progress has been made in understanding the relationship between xylem structure and cohesion-tension water transport. The mechanism of cavitation and its linkage to pit structure is now relatively well understood. The development of methods for quantifying cavitation has made ecological studies possible, and these have revealed links between xylem anatomy and ecology. In particular, the major structure-function trade-offs and trends with respect to freezing- and drought-induced cavitation have been characterized. It is now well established that hydraulic constraints, which are at least in part related to xylem structure, have a major impact on gas exchange and plant water use. Roots, especially small roots, have been identified as a weak link in the hydraulic continuum under drought conditions. Models based on the hydraulics of the soil-plant continuum have the potential for mechanistically linking canopy gas exchange capability with the architecture of the root system, and the characteristics of the soil (Jackson *et al.* 2000). These should help predict how patterns of plant water use will respond to climatic change.

Future research has the opportunity to build in two very different, but complimentary directions. Working up in scale from the xylem there are promising links between plant hydraulics and ecosystem functioning as repre-

sented by a variety of modelling approaches (e.g. West *et al.* 1997; Sperry *et al.* 1998). Continued refinement and extension of such models will help us understand broader patterns in productivity and vegetation that are related to plant water use. Moving down in scale, there is much to be learned about refilling phenomena in response to cavitation, and how this is related to xylem structure. In particular, reports of refilling under negative pressure (Salleo *et al.* 1996; Zwieniecki & Holbrook 1998; Tyree *et al.* 1999; Holbrook *et al.* 2001) deserve more attention, and if confirmed, must be explained in terms of xylem structure and physiology. The functional significance of many aspects of structure remains to be quantified and demonstrated. Variation in perforation plates, vessel element lengths, wall sculpturing, pitting types (including vestured pits), conduit groupings, fiber and xylem parenchyma structure and distribution all await a strong linkage to the function of xylem in transport. New techniques like the vessel casting method (André 1993, 2001) could be useful in this regard. The recent quantitative linkage between wood density and conduit structure to the resistance of conduit collapse will hopefully inspire more attention towards this simple, but fundamental function of the xylem network. The speculations of Carlquist and others along these lines (e.g. Carlquist 1988) that were dismissed by Zimmermann (1983) deserve a closer look using the appropriate biomechanical tests. Finally, very little is known of the genetic *vs* environmental controls on cavitation resistance and xylem conductivity, and how this is translated via modifications in xylem structure. Martin Zimmermann's approach of combining anatomical data with an experimental approach will continue to yield new insights into the field of xylem structure and function.

References

Alder, N.N., Sperry, J.S. & Pockman, W.T. (1996) Root and stem xylem embolism, stomatal conductance and leaf turgor in *Acer grandidentatum* populations along a soil moisture gradient. *Oecologia,* **105,** 293–301.

Ameglio, T., Ewers, F.W., Cochard, H., Martignac, M., Vandame, M., Bodet, C. & Cruiziat, P. (2001) Winter stem xylem pressure in walnut trees: effect of carbohydrates, cooling and freezing. *Tree Physiology,* **21,** 387–394.

André, J.-P. (1993) Micromoulage des espaces vides intra et intercellulaires dans les tissus végétaux. *Comptes rendus de l'Académie des Sciences Paris,* **316,** 1336–1341.

André, J.-P. (2001) Heterogenous, branched, zigzag and circular vessels: unexpected but frequent forms of tracheary element files: description-localization-formation. *Cell & Molecular Biology of Wood Formation* (eds. R. Savidge, J. Barnett & R. Napier), pp. 387–395. BIOS Scientific Publishers, Oxford.

Baas, P. (1986) Ecological patterns in xylem anatomy. *On the Economy of Plant Form and Function* (ed. T.J. Givnish), pp. 327–349. Cambridge University Press, Cambridge.

Böhm, J. (1893) Kapillarität und Saftsteigen. *Berichte der Deutschen Botanischen Gesellschaft,* **11,** 506–515.

Boorse, G.C., Ewers, F.W. & Davis, S.D. (1998) Response of chaparral shrubs to below-freezing temperatures: acclimation, ecotypes, seedlings vs. adults. *American Journal of Botany,* **85,** 1224–1230.

Braun, H.J. (1970) Funktionelle Histologie der sekundären Sproßachse. I. Das Holz. *Handbuch der Pflanzenanatomie* (eds. W. Zimmermann, P. Ozenda & H.D. Wulff), 2nd edn, pp. 1–190. Bornträger, Berlin.

Braun, H.J. (1984) The significance of the accessory tissues of the hydrosystem for osmotic water shifting as the second principle of water ascent, with some thoughts concerning the evolution of trees. *International Association of Wood Anatomists Bulletin,* **5,** 275–294.

Brodribb, T. & Hill, R.S. (1999) The importance of xylem constraints in the distribution of conifer species. *New Phytologist,* **143,** 365–372.

Calkin, H.W., Gibson, A.C. & Nobel, P.S. (1986) Biophysical model of xylem conductance in tracheids of the fern *Pteris vitata. Journal of Experimental Botany,* **37,** 1054–1064.

Carlquist, S. (1988) *Comparative Wood Anatomy.* Springer, Berlin.

Chiu, S.T. & Ewers, F.W. (1993) The effect of segment length on conductance measurements in *Lonicera fragrantissima. Journal of Experimental Botany,* **44,** 175–181.

Choat, B., Holtum, J.A.M., Luly, J.G. & Ball, M.C. (2000) Hydraulic architecture of seasonally dry rainforest species of differing leaf phenology from North Queensland, Australia. *Ecological Society of America – Abstracts of 85th Annual Meeting,* p. 73.

Cochard, H. & Tyree, M.T. (1990) Xylem dysfunction in *Quercus*: vessel sizes, tyloses, cavitation and seasonal changes in embolism. *Tree Physiology,* **6,** 393–407.

Cochard, H., Bodet, C., Ameglio, T. & Cruiziat, P. (2000) Cryo-scanning electron microscopy observations of vessel content during transpiration in walnut petioloes. Facts or artifacts? *Plant Physiology,* **124,** 1191–1202.

Cochard, H., Lemoine, D., Ameglio, T. & Granier, A. (2001) Mechanisms of xylem recovery from winter embolism in *Fagus sylvatica. Tree Physiology,* **21,** 27–33.

Comstock, J.P. & Sperry, J.S. (2000) Theoretical considerations of optimal conduit length for water transport in vascular plants. *New Phytologist,* **148,** 195–218.

Davis, S.D., Sperry, J.S. & Hacke, U.G. (1999a) The relationship between xylem conduit diameter and

cavitation caused by freezing. *American Journal of Botany*, **86,** 1367–1372.

Davis, S.D., Ewers, F.W., Wood, J.J., Reeves, K.J. & Kolb, K.J. (1999b) Differential susceptibility to xylem cavitation among three pairs of *Ceanothus* species in the Transverse Mountain ranges of southern California. *Écoscience*, **6,** 180–186.

Dixon, H.H. & Joly, J. (1895) On the ascent of sap. *Philosophical Transactions of the Royal Society of London B*, **186,** 563–576.

Ellmore, G.S. & Ewers, F.W. (1986) Fluid flow in the outermost xylem increment of a ring-porous tree, *Ulmus americana. American Journal of Botany*, **73,** 1771–1774.

Enquist, B.J., West, G.B. & Brown, J.H. (2000) Quarter-power allometric scaling in vascular plants: functional basis and ecological consequences. *Scaling in Biology* (eds. J.H. Brown & G.B. West), pp. 167–198. Oxford University Press, Oxford.

Ewers, F.W. (1985) Xylem structure and water conduction in conifer trees, dicot trees, and lianas. *International Association of Wood Anatomists Bulletin*, **6,** 309–317.

Ewers, F.W. & Fisher, J.B. (1989) Variation in vessel length and diameter in stems of six tropical and subtropical lianas. *American Journal of Botany,* **76,** 1452–1459.

Ewers, F.W., Cochard, H. & Tyree, M.T. (1997a) A survey of root pressures in vines of a tropical lowland forest. *Oecologia* **110,** 191–196.

Ewers, F.W., Carlton, M.R., Fisher, J.B., Kolb, K.J. & Tyree, M.T. (1997b) Vessel diameters in roots versus stems of tropical lianas and other growth forms. *International Association of Wood Anatomists Journal,* **18,** 261–279.

Feild, T.S. & Brodribb, T. (2001) Stem water transport and freeze-thaw xylem embolism in conifers and angiosperms in a Tasmanian treeline heath. *Oecologia,* **127,** 314–320.

Hacke, U.G. (2000) Sap ascent in plants. *Tree Sap II* (ed. M. Terazawa), pp. 59–66. Hokkaido University Press, Sapporo.

Hacke, U. & Sauter, J.J. (1995) Vulnerability of xylem to embolism in relation to leaf water potential and stomatal conductance in *Fagus sylvatica* f. *purpurea* and *Populus balsamifera. Journal of Experimental Botany,* **46,** 1177–1183.

Hacke, U. & Sauter, J.J. (1996a) Xylem dysfunction during winter and recovery of hydraulic conductivity in diffuse-porous and ring-porous trees. *Oecologia,* **105,** 435–439.

Hacke, U. & Sauter, J.J. (1996b) Drought-induced xylem dysfunction in petioles, branches, and roots of *Populus balsamifera* L. and *Alnus glutinosa* (L.) Gaertn. *Plant Physiology,* **111,** 413–417.

Hacke, U.G., Sperry, J.S., Ewers, B.E., Ellsworth, D.S., Schäfer, K.V.R. & Oren, R. (2000a) Influence of soil porosity on water use in *Pinus taeda. Oecologia* **124,** 495–505.

Hacke, U.G., Sperry, J.S. & Pittermann, J. (2000b) Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. *Basic and Applied Ecology,* **1,** 31–41.

Hacke, U.G., Stiller, V., Sperry, J.S., Pittermann, J. & McCulloh, K. (2001a) Cavitation fatigue: embolism and refilling cycles can weaken the cavitation resistance of xylem. *Plant Physiology,* **125,** 779–786.

Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D. & McCulloh, K. (2001b) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia,* **126,** 457–461.

Hammel, H.T. (1967) Freezing of xylem sap without cavitation. *Plant Physiology,* **42,** 55–66.

Holbrook, N.M., Ahrens, E.T., Burns, M.J. & Zwieniecki, M.A. (2001) In vivo observation of cavitation and embolism repair using magnetic resonance imaging. *Plant Physiology,* **126,** 27–31.

Jackson, R.B., Sperry, J.S. & Dawson, T.E. (2000) Root water uptake and transport: scaling physiological processes for global predictions. *Trends in Plant Science,* **5,** 482–488.

Jarbeau, J.A., Ewers, F.W. & Davis, S.D. (1995) The mechanism of water stress induced xylem dysfunction in two species of chaparral shrubs. *Plant, Cell and Environment,* **18,** 189–196.

Kolb, K.J. & Sperry, J.S. (1999) Transport constraints on water use by the Great Basin shrub, *Artemisia tridentata. Plant, Cell and Environment,* **22,** 925–936.

Kramer, P.J. & Boyer, J.S. (1995) *Water Relations of Plants and Soils.* Academic Press, San Diego.

Langan, S.J., Ewers, F.W. & Davis, S.D. (1997) Xylem dysfunction caused by water stress and freezing in two species of co-occurring chaparral shrubs. *Plant, Cell and Environment,* **20,** 425–437.

Lemoine, D., Granier, A. & Cochard, H. (1999) Mechanism of freeze-induced embolism in *Fagus sylvatica* L. *Trees,* **13,** 206–210.

Lösch, R. (2001) *Wasserhaushalt der Pflanzen.* Quelle & Meyer, Wiebelsheim.

Marvin, J.W. & Greene, M.T. (1951) Temperature-induced sap flow in excised stems of *Acer. Plant Physiology,* **26,** 565–580.

Mencuccini, M. & Comstock, J. (1997) Vulnerability to cavitation in populations of two desert species, *Hymenoclea salsola* and *Ambrosia dumosa*, from different climatic regions. *Journal of Experimental Botany,* **48,** 1323–1334.

Milburn, J.A. (1973) Cavitation studies on whole *Ricinus* plants by acoustic detection. *Planta,* **112,** 333–342.

Milburn, J.A. (1996) Sap ascent in vascular plants: challengers to the cohesion theory ignore the significance of immature xylem and recycling of Münch water. *Annals of Botany,* **78,** 399–407.

Münch, E. (1930) *Die Stoffbewegungen in der Pflanze.* Fischer, Jena.

Nardini, A. & Salleo, S. (2000) Limitation of stomatal conductance by hydraulic traits: sensing or preventing xylem cavitation? *Trees* **15,** 14–24.

Nobel, P.S. (1999) *Physicochemical and Environmental Plant Physiology,* 2nd ed. Academic Press, San Diego.

North, G.B., Ewers, F.W. & Nobel, P.S. (1992) Main root-lateral root junctions of two desert succulents: Changes in axial and radial components of hydraulic conductivity during drying. *American Journal of Botany,* **79,** 1039–1050.

Pinol, J. & Sala, A. (2000) Ecological implications of xylem cavitation for several Pinaceae in the pacific Northern USA. *Functional Ecology*, **14,** 538–545.

Pockman, W.T. & Sperry, J.S. (1997) Freezing-induced xylem cavitation and the northern limit of *Larrea tridentata. Oecologia*, **109,** 19–27.

Pockman, W.T. & Sperry, J.S. (2000) Vulnerability to cavitation and the distribution of Sonoran Desert vegetation. *American Journal of Botany,* **87,** 1287–1299.

Rood, S.B., Patino, S., Coombs, K. & Tyree, M.T. (2000) Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. *Trees,* **14,** 248–257.

Salleo, S., LoGullo, M.A. & Oliveri, F. (1985) Hydraulic parameters measured in 1-year-old twigs of some Mediterranean species with diffuse-porous wood. *Journal of Experimental Botany,* **36,** 1–11.

Salleo, S., LoGullo, M.A., De Paoli, D. & Zippo, M. (1996) Xylem recovery from cavitation-induced embolism in young plants of *Laurus nobilis*: a possible mechanism. *New Phytologist*, **132,** 47–56.

Sauter, J.J. (1984) Detection of embolization of vessels by a double staining technique. *Journal of Plant Physiology,* **116,** 331–342.

Sauter, J.J., Iten, W. & Zimmermann, M.H. (1973) Studies on the release of sugar into the vessels of sugar maple (*Acer saccharum*). *Canadian Journal of Botany,* **51,** 1–8.

Shane, M.W., McCully, M.E. & Canny, M.J. (2000) Architecture of branch-root junctions in maize: structure of the connecting xylem and porosity of pit membranes. *Annals of Botany,* **85,** 613–624.

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

Sperry, J.S. (1995) Limitations of stem water transport and their consequences. *Plant Stems: Physiology and Functional Morphology* (ed. B. Gartner), pp. 105–124. Academic Press, San Diego.

Sperry, J.S. & Robson D.J. (2001) Xylem cavitation and freezing in conifers. *Conifer Cold Hardiness* (eds. F.J. Bigras & S.J. Colombo), pp. 121–136. Kluwer Academic, Dordrecht.

Sperry, J.S. & Saliendra, N.Z. (1994) Intra- and interplant variation in xylem cavitation in *Betula occidentalis. Plant, Cell and Environment,* **17,** 1233–1241.

Sperry, J.S. & Sullivan, J.E.M. (1992) Xylem embolism in response to freeze-thaw cycles and water stress in ring-porous, diffuse-porous, and conifer species. *Plant Physiology,* **100,** 605–613.

Sperry, J.S. & Tyree, M.T. (1990) Water stress induced xylem cavitation in three species of conifers. *Plant, Cell and Environment,* **13,** 427–436.

Sperry, J.S., Holbrook, N.M., Zimmermann, M.H. & Tyree, M.T. (1987) Spring filling of xylem vessels in wild grapevine. *Plant Physiology*, **83,** 414–417.

Sperry, J.S., Donnelly, J.R. & Tyree, M.T. (1988a) A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell and Environment*, **11,** 35–40.

Sperry, J.S., Donnelly, J.R. & Tyree, M.T. (1988b) Seasonal occurrence of xylem embolism in sugar maple (*Acer saccharum*). *American Journal of Botany,* **75,** 1212–1218.

Sperry, J.S., Nichols, K.L., Sullivan, J.E.M. & Eastlack, S.E. (1994) Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. *Ecology*, **75,** 1736–1752.

Sperry, J.S., Saliendra, N.Z., Pockman, W.T., Cochard, H., Cruiziat, P., Davis, S.D., Ewers, F.W. & Tyree, M.T. (1996) New evidence for large negative xylem pressures and their measurement by the pressure chamber method. *Plant, Cell and Environment,* **19,** 427–436.

Sperry, J.S., Adler, F.R., Campbell, G.S. & Comstock, J.P. (1998) Limitation of plant water use by rhizosphere and xylem conductances: results from a model. *Plant, Cell and Environment,* **21,** 347–359.

Sperry, J.S., Hacke, U.G., Comstock, J.P. & Oren, R. (in press) Water deficits and hydraulic limits to leaf water supply. *Plant, Cell and Environment.*

Steudle, E. (2001) The cohesion-tension mechanism and the acquisition of water by plant roots. *Annual Review of Plant Physiology and Molecular Biology,* **52,** 847–875.

Tibbetts, T.J. & Ewers, F.W. (2000) Root pressure and specific conductivity in temperate lianas: exotic *Celastrus orbiculatus* (Celastraceae) vs. native *Vitis riparia* (Vitaceae). *American Journal of Botany,* **87,** 1272–1278.

Tyree, M.T. (1997) The cohesion-tension theory of sap ascent: current controversies. *Journal of Experimental Botany,* **48,** 1753–1765.

Tyree, M.T. & Sperry, J.S. (1989) The vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology*, **40,** 19–38.

Tyree, M.T., Cochard, H., Cruiziat, P., Sinclair, B. & Ameglio, T. (1993) Drought-induced leaf shedding in walnut: evidence for vulnerability segmentation. *Plant, Cell and Environment,* **16,** 879–882.

Tyree, M.T., Davis, S.D. & Cochard, H. (1994) Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? *International Association of Wood Anatomists Journal,* **15,** 335–360.

Tyree, M.T., Salleo, S., Nardini, A., Assunta, M., Lo Gullo, M.A. & Mosca, R. (1999) Refilling of embolized vessels in young stems of laurel. Do we need a new paradigm? *Plant Physiology*, **120,** 11–22.

Utsumi, Y., Sano, Y., Fujikawa, S., Funada, R. & Ohtani, J. (1998) Visualization of cavitated vessels in winter and refilled vessels in diffuse-porous trees by cryo-scanning electron microscopy. *Plant Physiology,* **117,** 1463–1471.

Utsumi, Y., Sano, Y., Funada, R., Fujikawa, S. & Ohtani, J. (1999) The progression of cavitation in earlywood vessels of *Fraxinus mandshurica* var. *japonica* during freezing and thawing. *Plant Physiology,* **121,** 897–904.

Van Bel, A.J.E (1999) Evolution, polymorphology, and multifunctionality of the phloem system. *Perspectives in Plant Ecology, Evolution and Systematics,* **2,** 163–184.

Van Ieperen, W., van Meeteren, U. & van Gelder, H. (2000) Fluid ionic composition influences hydraulic conductance of xylem conduits. *Journal of Experimental Botany,* **51,** 769–776.

Wang, J., Ives, N.E. & Lechowicz, M.J. (1992) The relation of foliar phenology to xylem embolism in trees. *Functional Ecology,* **6**, 469–475.

West, G.B., Brown, J.H. & Enquist, B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science,* **276**, 122–126.

West, N.E. (1989) Intermountain deserts, shrub steppes, and woodlands. *North American Terrestrial Vegetation* (eds. M.G. Barbour & W.D. Billings),

pp. 209–230. Cambridge University Press, Cambridge.

Woodcock, D.W., Dos Santos, G. & Reynel, C. (2000) Wood characteristics of Amazon forest types. *International Association of Wood Anatomists Journal* **21,** 277–292.

Zhu, X.B., Cox, R.M. & Arp, P.A. (2000) Effects of xylem cavitation and freezing injury on dieback of yellow birch (*Betula alleghaniensis*) in relation to a simulated winter thaw. *Tree Physiology,* **20**, 541–547.

Zimmermann, M.H. (1978) Hydraulic architecture of some diffuse-porous trees. *Canadian Journal of Botany,* **56,** 2286–2295.

Zimmermann, M.H. (1983) *Xylem Structure and the Ascent of Sap.* Springer, Berlin.

Zimmermann, M.H. & Jeje, A.A. (1981) Vessel-length distribution of some American woody plants. *Canadian Journal of Botany,* **59,** 1882–1892.

Zimmermann, M.H. & Potter, D. (1982) Vessel-length distribution in branches, stem, and roots of *Acer rubrum. International Association of Wood Anatomists Bulletin,* **3,** 103–109.

Zwieniecki, M.A. & Holbrook, N.M. (1998) Diurnal variation in xylem hydraulic conductivity in white ash (*Fraxinus americana* L.) and red maple (*Acer rubrum* L.) and red spruce (*Picea rubens* Sarg.). *Plant, Cell and Environment,* **21,** 1173–1180.

Zwieniecki, M.A., Melcher, P.J. & Holbrook, N.M. (2001) Hydrogel control of xylem hydraulic resistance in plants. *Science,* **291,** 1059–1062.