Review

Water transport in trees: current perspectives, new insights and some controversies

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Abstract

This review emphasizes recent developments and controversies related to the uptake, transport and loss of water by trees. Comparisons of the stable isotope composition of soil and xylem water have provided new and sometimes unexpected insights concerning spatial and temporal partitioning of soil water by roots. Passive, hydraulic redistribution of water from moister to drier portions of the soil profile via plant root systems may have a substantial impact on vertical profiles of soil water distribution, partitioning of water within and among species, and on ecosystem water balance. The recent development of a technique for direct measurement of pressure in individual xylem elements of intact, transpiring plants elicited a number of challenges to the century-old cohesion–tension theory. The ongoing debate over mechanisms of long-distance water transport has stimulated an intense interest in the phenomenon and mechanisms of embolism repair. Rather than embolism being essentially irreversible, it now appears that there is a dynamic balance between embolism formation and repair throughout the day and that daily release of water from the xylem via cavitation may serve to stabilize leaf water balance by minimizing the temporal imbalance between water supply and demand. Leaf physiology is closely linked to hydraulic architecture and hydraulic perturbations, but the precise nature of the signals to which stomata respond remains to be elucidated. When water transport in trees is studied at multiple scales from single leaves to the whole organism, considerable functional convergence in regulation of water use among phylogenetically diverse species is revealed. © Published by Elsevier Science B.V.

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1. Introduction

Trees are an appealing system for studying long-distance water transport in plants. In the largest individuals, water may traverse a tortuous pathway more than 100 m long from the point where it is taken up in the soil to the sites of

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evaporation in the leaves. The integrity of their water transport system faces increasing challenges as trees develop from small seedlings to adults. Trees present a broad range of hydraulic architecture from starkly simple to bafflingly complex, and interactions between hydraulic architecture and physiological regulation of water transport at the leaf, whole-tree and intermediate scales are not fully understood. In contrast with most herbaceous plants, the voluminous secondary xylem of large trees can introduce a significant storage component to their water budget, thereby complicating the interpretation of patterns of water flow through their stems and its relationship to evaporation from leaves. Trees thus present a challenge to plant biologists to understand the integration of activities in such large organisms.

The following is not intended to be a comprehensive review of water transport in trees. Rather, we have elected to define and cover five topics based on one or more of the following criteria: significant recent insights or technical developments, recent intensive research activity, and recent controversy. Because water has to be acquired by the roots before it can be moved to the top of the tree, the first topic deals with partitioning and redistribution of soil water by roots.

2. Spatial and temporal partitioning of soil water uptake

Partitioning of soil water uptake among individuals of different species, or among individuals of different size classes of the same species, may reduce competition between co-occurring trees for the same limited water resources. Soil water partitioning can result from temporal or spatial displacement of water uptake, or from a combination of both. Temporal partitioning of soil water can be achieved through seasonal displacement of leaf expansion and leaf fall, the relative rates and timing of which largely determine the potential rate of transpirational water loss. Spatial partitioning of soil water may occur along a vertical axis, corresponding to differences in the abundance of active roots, and along a

horizontal axis defined by the pattern of species distribution and spacing (Hinckley et al., 1991). For example, wide spacing between woody tropical Savanna species reduces competition for limited soil water resources during the prolonged dry season (Goldstein and Sarmiento, 1986).

2.1. Stable isotope studies

The source regions of soil water uptake by plants have traditionally been difficult to assess (Ehleringer and Dawson, 1992). Excavation of roots to determine their spatial distribution is destructive, time consuming, and impractical in some ecosystems such as tropical forests because of their high species diversity and high woody plant density. Furthermore, the mere presence of roots at a given depth in the soil profile is not necessarily a reliable indicator of their relative contribution to total water uptake (Ehleringer and Dawson, 1992). The development of stable isotope techniques has greatly facilitated the characterization of sources of water at different depths in the soil profile. Analysis of the natural stable hydrogen (D, H) or oxygen (^{18}O, ^{16}O) isotope composition of soil and xylem water allows differential access to soil water pools to be inferred without the invasive excavation of root systems (Ehleringer and Dawson, 1992; Sternberg and Swart, 1987). The isotopic composition of the soil water may vary with depth because each successive precipitation event has a distinct isotopic signature and/or because water near the soil surface becomes enriched in the heavier isotopes as a result of evaporative fractionation (Allison, 1982; Allison and Hughes, 1983). Seasonal variation in the isotopic composition of precipitation is typically greater in temperate than in tropical regions (Yurtsever and Gat, 1981). Therefore, in tropical sites experiencing a prolonged dry season, evaporative fractionation is often the major determinant of variation in the isotopic composition of soil water with depth (Jackson et al., 1995, 1999; Meinzer et al., 1999a). If the isotopic signatures of surface and groundwater are distinct, their relative utilization can be estimated from the isotopic composition of the xylem water using a simple linear mixing model (White et al., 1985).

Soil water-partitioning studies carried out using stable isotope techniques often yield results that are somewhat counterintuitive or unexpected at first sight. For example, Valentini et al. (1992) found that evergreen Mediterranean species tended to rely on rainwater while deciduous species relied almost exclusively on more dependable groundwater, Dawson and Ehleringer (1991) concluded that streamside trees actually used little stream water, Le Roux et al. (1995) discovered that both grass and woody species used water from the upper layers of the soil profile during the dry and wet seasons in a West African humid Savanna, and we have found that deciduous Brazilian Cerrado tree species have access to deeper sources of soil water than evergreen species (Jackson et al., 1999). As expected, larger trees have been shown to preferentially tap deeper sources of soil water than smaller trees (Dawson, 1996), but the reverse has also been reported (Meinzer et al., 1999a). Pulse chase experiments involving surface irrigation of plots with deuterated water have recently been used to determine patterns of root water uptake with depth (Moreira et al., 2000). This approach may reduce uncertainties associated with complex patterns of stable isotope distribution in the soil water of tropical regions.

In tropical regions with a distinct dry season and minimal seasonal temperature changes, co-occurring tree species may exhibit a wide array of seasonal patterns of leaf production and other growth related activities (Wright, 1996; Meinzer et al., 1999a). These annual growth patterns are not always synchronized with seasonal changes in soil water availability. It is therefore likely that in seasonally dry tropical forests, competition for limited soil water during the dry season is reduced by species-specific differences in leaf phenology in addition to differences in rooting patterns and root activity. In a Hawaiian dry forest, for example, leaf phenology ranged from dry season deciduous at one extreme, to evergreen with near constant leaf expansion rates at the other. The species with the greatest annual variability in leaf expansion rates, paradoxically tended to tap the deepest soil water sources as reflected in their more negative xylem sap δD values (Fig. 1). Con-

versely, species with root systems restricted to potentially less abundant water sources in the upper portion of the soil profile, tended to exhibit more moderate variation in leaf expansion rates (Stratton et al., 2000a).

Even within the same species, source water utilization (spatial partitioning) can shift seasonally. For example, in a seasonally dry forest in Panama, trees able to exploit progressively deeper sources of soil water during the dry season, as indicated by increasingly negative xylem δD values, were also able to maintain constant or even increase rates of water use (Meinzer et al., 1999a). Seasonal courses of water use and soil water partitioning were also associated with leaf phenology. Species with the smallest seasonal variability in leaf fall tapped increasingly deep sources of soil water as the dry season progressed (Fig. 2). Dawson and Pate (1996) also observed seasonal shifts in source water utilization among Australian phreatophytic species with dimorphic root systems.
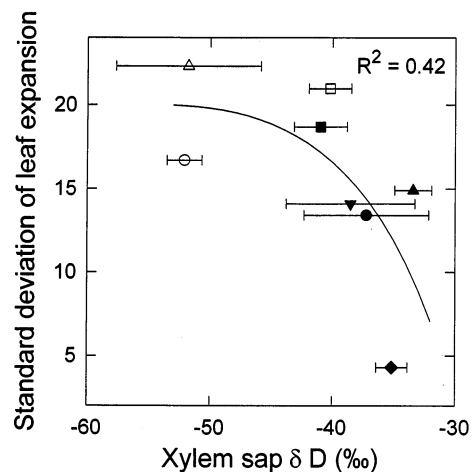

Fig. 1. Seasonal variability in leaf expansion (estimated as standard deviation of leaf production) in relation to xylem sap δD for eight Hawaiian dry forest woody species. Symbols: ▲, *Pouteria sandwicensis*; △, *Reynoldsia sandwicensis*; ■, *Nestegis sandwicensis*; □, *Schinus terebinthifolius*; ●, *Diospyros sandwicensis*; ○, *Metrosideros polymorpha*; ◆, *Myoporum sandwicense*; ▼, *Nesoluma polynesicum*. Adapted from Stratton et al. (2000a).
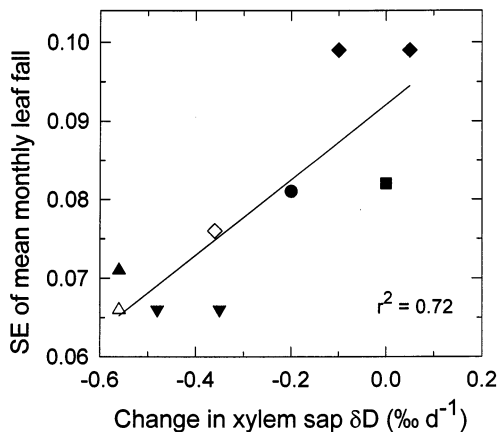
Fig. 2. Standard error of mean monthly leaf fall in relation to average daily change in xylem sap δD during the dry season for individuals of seven tree species growing on Barro Colorado Island, Panama. A negative change in δD indicates that xylem sap δD decreased from the beginning to the end of the dry season. Symbols: ■, *Cordia alliodora*; ●, *Jacaranda copaia*; ◇, *Anacardium excelsum*; ▼, *Trichilia tuberculata*; △, *Luehea seemannii*; ▲, *Quararibea asterolepis*; ◆, *Alseis blackiana*. Adapted from Meinzer et al. (1999a).

2.2. Hydraulic redistribution

Vertical profiles of soil water distribution with depth may be more influenced by the activities of plants than previously thought. The movement of water from moister to drier portions of the soil profile via plant root systems has been termed hydraulic lift (Corak et al., 1987; Richards and Caldwell, 1987; Caldwell and Richards, 1989). The direction of water movement is typically upward, towards the shallower soil layers. However, recent measurements of sap flow in taproots and lateral roots of trees have demonstrated that roots can also redistribute water from the surface to deeper soil layers (Burgess et al., 1998; Sakuratani et al., 1999; Smith et al., 1999). The process is thought to be largely passive, requiring only a gradient in soil water potential (Ψ_s), a more positive Ψ in the root xylem than in surrounding dry soil layers, and a relatively low resistance to reverse flow from the roots. Because it can be bi-directional and is apparently passive, 'hydraulic redistribution' has been proposed as a more comprehensive term for the phenomenon (Burgess et al., 1998). Hydraulic lift usually occurs at night when transpiration has diminished sufficiently to allow the water potential in the roots to exceed that in the drier portions of the soil profile. Evidence for hydraulic lift consists largely of time courses of Ψ_s showing increasing Ψ in drier soil layers during the night or other periods when transpiration is reduced (Richards and Caldwell, 1987; Dawson, 1993; Millikin Ishikawa and Bledsoe, 2000). Deuterated water supplied to deep roots of shrubs has also been used as a label to trace movement of water to shallow roots of grasses (Caldwell and Richards, 1989). More recently, the measurement of water movement within the roots with heat pulse techniques has been used to assess the magnitude of hydraulic redistribution of soil water (Burgess et al., 1998). Based on this and other evidence, it is believed that hydraulic lift can contribute significantly to the water balance of not only the plant responsible for it, but also neighboring plants of other species (Dawson, 1996). In addition to its positive influence on plant water balance during dry periods, hydraulic redistribution may enhance availability of nutrients in shallow soil layers and facilitate the uptake of nutrients by shallow, fine roots (Caldwell et al., 1998) and the growth of tap roots into dryer soil layers (Schulze et al., 1998). Now that more than 60 cases of hydraulic lift have been demonstrated (Jackson et al., 2000), there is no reason to doubt that its existence is more widespread wherever conditions are conducive to its occurrence. However, the significance of hydraulic lift for ecosystem-level water fluxes remains to be evaluated.

3. Long-distance water transport

3.1. The cohesion–tension theory

Curiosity about how water is moved to the tops of tall trees goes back centuries (e.g. Hales, 1727). The Cohesion–Tension (C–T) theory, proposed in the late 19th century by Dixon and Joly (1894), has become the most widely accepted explanation of the mechanism of the ascent of sap. It holds that the driving force for water movement is generated by transpirational water loss, which

transmits tension through continuous water columns running from the evaporating surfaces in the leaves to the roots. According to the C–T theory, the minimum vertical xylem tension gradient should be 0.01 MPa m^{-1} when transpiration is absent. When transpiration is occurring, frictional resistances are expected to cause considerably larger tensions to be generated, especially in plants growing in dry soils. The C–T theory has prevailed largely unmodified for > 100 years, a somewhat unusual situation for a scientific paradigm explaining a fundamental process. A few early tests using indirect methods yielded results consistent with the presence of tension in the xylem (Renner, 1912, 1925; Ursprung and Blum, 1916; Nordhausen, 1919), but it was not until the 1960's with the development of the pressure chamber (Scholander et al., 1965) that the predominance of theory seemed assured.

Until recently, the periodic introduction of alternative theories explaining long-distance water transport (Plumb and Bridgman, 1972; Amin, 1982; Braun, 1984) had elicited little response, largely because massive amounts of data collected with the pressure chamber seemed to be consistent with the C–T theory. Beginning in about 1990, however, challenges to cohesion–tension as the sole mechanism by which water ascends have stimulated a lively debate in a field previously characterized by a dangerous degree of complacency. The debate was triggered by the development of the xylem pressure probe (XPP), which allowed pressure or tension to be measured directly in individual vessels of intact plants for the first time (Balling and Zimmermann, 1990; Benkert et al., 1991). Although measurements with the XPP confirmed the existence of tension in the xylem of intact, transpiring plants, the tensions often seemed too small to be compatible with water transport being entirely tension-driven (Benkert et al., 1991; Zimmermann et al., 1993, 1994; Benkert et al., 1995), and were often much smaller than tensions inferred from indirect measurements made with the pressure chamber. These results evoked considerable scepticism concerning the validity of the XPP technique (e.g. Pockman et al., 1995; Milburn, 1996; Sperry et al., 1996), despite the rigorous and exhaustive tests to which

it was subjected during its development (Zimmermann et al., 1995). Although maximum tensions measurable with the XPP are limited by cavitation within the probe itself, it was shown that contrary to initial fears, the mere insertion of the probe into a xylem element does not automatically provoke cavitation. Acceptance of the XPP technique has increased as a result of subsequent studies showing that xylem tensions measured with the XPP agree with those inferred from the pressure chamber, albeit over a relatively narrow range and under specific conditions (Melcher et al., 1998; Wei et al., 1999). However, serious problems in reconciling measurements made with the XPP and pressure chamber remain mainly because the measurement range of the pressure chamber extends beyond that of current versions of the XPP. For example, the largest stable tensions measured with the XPP to date are of the order of 1.0 MPa, whereas tensions approaching 5–7 MPa are routinely inferred from balance pressures obtained with the pressure chamber. Furthermore, samples placed in the pressure chamber may contain a large fraction of woody tissue, whereas measurements with the XPP have been confined to leaf veins and petioles, and fleshy portions of stems and roots because the delicate glass microcapillary of the XPP is not capable of penetrating woody tissue. It is not known to what extent the sometimes-large discrepancies between measurements made with the XPP and the pressure chamber may be attributable to differences in regulation of xylem pressure in leaves and adjacent woody stems.

Although the pressure chamber remains a valuable tool for characterizing tree water relations, there are important constraints on interpretation of the balance pressures obtained. These were recognized soon after the technique was introduced (Begg and Turner, 1970; Ritchie and Hinckley, 1971; Janes and Gee, 1973; Turner and Long, 1980) but need to be re-emphasized. Perhaps the most serious constraint is the inability of the pressure chamber to measure xylem pressure under nonequilibrium conditions (i.e. in transpiring leaves). Substantial hydraulic resistances in leaves can cause steep water potential gradients to develop in response to transpirational water

movement (Yang and Tyree, 1994; Melcher et al., 1998). Under these conditions, excision of a rapidly transpiring leaf will cause the tension in the xylem to re-equilibrate to a value between that of the water potential of the bulk leaf tissue and the original in situ value of tension. The post-excision value of xylem tension deduced with the pressure chamber will approximate the water potential of the bulk leaf tissue rather than the pre-excision xylem tension because $< 10\%$ of the leaf water is usually contained in the xylem. Indeed, it has long been noted that large differences in balance pressure can be observed between adjacent transpiring leaves and covered, non-transpiring leaves (Ritchie and Hinckley, 1971; Turner and Long, 1980; Saliendra and Meinzer, 1989). The non-transpiring leaf should function as a tensiometer, permitting the xylem pressure of the stem and remaining nearby leaves to be estimated from its balance pressure if water columns are continuous throughout the plant and if local variations in xylem tension are negligible (Passioura 1982; McCutchan and Shackel, 1992). The inability of the pressure chamber to reliably measure xylem pressure in transpiring leaves can lead to errors in characterizing the driving forces and therefore the mechanisms involved in long-distance water transport. Nevertheless, the pressure chamber can still be considered as the technique of choice for obtaining valid estimates of volume-averaged leaf water potential in intact plants.

The large body of evidence consistent with tension-driven water transport includes numerous demonstrations that water in xylem tissue can sustain substantial tensions before cavitating (Pockman et al., 1995; Sperry et al., 1996), direct measurements of tension with the XPP, and indirect measurements with the pressure chamber of tension in non-transpiring leaves. Nevertheless, as indicated above, some observations appear to be in conflict with the idea that long-distance water transport is exclusively tension-driven. In tall trees, for example, the assumptions of the C–T theory require that xylem tension increase according to a minimum gravitational gradient of 0.01 MPa for every 1 m increase in height. Regardless of a tree's hydraulic architecture and whether or not transpiration is occurring, if the xylem tension

at, for example, 30 m height is smaller than the value of 0.3 MPa predicted from the C–T theory and root pressure is absent, tension exerted through continuous water columns cannot be the only force involved in moving water to 30 m height. Although some data obtained with the pressure chamber in tall trees appear to be consistent with the predicted gravitational tension gradient (Hellkvist et al., 1974; Connor et al., 1977), other results obtained with both the pressure chamber (Connor et al., 1977; Koch et al., 1994) and the XPP (Zimmermann et al., 1993) point to tensions smaller than those predicted from the C–T theory. Unfortunately, interpretation of both types of observations is often ambiguous if they are made when transpiration, soil water deficits, or osmotically-induced root pressure are present.

3.2. Alternative theories

The results obtained with the XPP and earlier observations in apparent conflict with the C–T theory prompted Canny to propose a new theory of long-distance water transport, the so-called 'compensating pressure' theory (Canny, 1995, 1998). Briefly, the theory holds that xylem tension is maintained within a stable range by a compensating pressure exerted by turgid living tissue surrounding the xylem. Furthermore, the compensating pressure is predicted to be instrumental in refilling embolized vessels by causing water to be extruded into them. In keeping with the lively exchange that had already been taking place prior to its introduction, the compensating pressure theory has been challenged in a series of strenuous critiques (Comstock, 1999; Tyree, 1999; Stiller and Sperry, 1999). Tyree (1999) has pointed out that tissue pressure can cause only a transitory increase in xylem pressure and therefore cannot be responsible for elevating xylem pressure during quasi steady-state water transport.

3.3. Conclusions and recommendations

Direct measurements with the xylem pressure probe have demonstrated that substantial tensions can develop in the xylem elements of transpiring

plants, implying that cohesion–tension is an important mechanism driving long-distance transport. However, reports of tensions apparently smaller than those expected from the C–T theory suggests that additional mechanisms may be involved and should be investigated. Less recent observations seemingly at odds with the C–T theory need to be explained, as they are numerous (Scholander et al., 1955, 1957, 1962) and there is no compelling reason to doubt their validity. As a beginning, vertical gradients in water potential should be reassessed in tall trees using independent techniques in parallel under unambiguous conditions consisting of high soil water content and the absence of transpiration and root pressure. Improved access to tall trees via canopy cranes and towers should make these types of measurements more feasible than they have been in the past.

Widely held ideas about operating ranges of xylem tension based on measurements with the pressure chamber on previously transpiring leafy shoots also need to be reassessed. Pressure chamber measurements should routinely be made on both covered and exposed leaves but even the covered leaf balance pressures can be ambiguous if substantial cavitation has occurred or if anatomy of the stem to which the leaf is attached allows water to be forced into nonconducting tissue during pressurization.

4. Xylem vulnerability and embolism repair

Water is transported in the xylem under tension (Dixon and Joly, 1894) and is therefore vulnerable to cavitation, the rapid expansion of a vacuum-filled space within a xylem conduit. Cavitation may be initiated during water stress by the entry of air through conduit pit membranes (the air-seeding hypothesis; Zimmermann, 1983), or by bubbles formed during freezing and thawing of xylem sap. The conduit quickly becomes filled with water vapor and air, resulting in an 'embolism' or blockage within the conduit. Embolism is of importance to trees because it results in reduced hydraulic conductivity, which could lead to increased tension and the possibility of further

'runaway' cavitation if transpiration continues at the same rate (Tyree and Ewers, 1991). Until recently, embolism was considered largely irreversible, slowly reversible over a time-scale of weeks or months (Sperry, 1995), or reversible under special conditions of high root (Tyree et al., 1986; Sperry et al., 1994) or stem pressure (Sperry et al., 1988b). Thus, because of its apparently irreversible nature in many woody plants, cavitation has traditionally been viewed as a serious dysfunction that must normally be avoided.

4.1. Brief history

Cavitation in water-stressed plants was first demonstrated by Milburn and Johnson (1966) using an acoustic recording technique that was later modified by Tyree and co-workers (Tyree and Dixon, 1983; Tyree and Sperry, 1989) to record at ultrasonic frequencies. The widely used method of assessing cavitation as the decline in hydraulic conductivity relative to conductivity after stems were flushed at high pressure to remove emboli was introduced in the 1980's (Sperry et al., 1988a). In some woody species, the acoustic emission and conductivity methods agree well, but in others cumulative acoustic emissions are a poor predictor of loss of conductivity because acoustic emissions are also generated during cavitation in non-conducting xylem cells (Sperry et al., 1988c). In addition to dehydration, positive pressure (Sperry and Tyree, 1990; Cochard et al., 1992; Salleo et al., 1992) and centrifugal force (Alder et al., 1997) were developed as methods to generate known pressure gradients for the study of xylem vulnerability to cavitation in excised organs and intact plants. Since the development of these methods, it has been shown that xylem cavitation in stems and roots is a common occurrence. The vulnerability of xylem to cavitation varies widely across taxa, and there is a close relationship between the degree of vulnerability and the minimum xylem water potential attained by each species (Milburn, 1991; Sperry, 1995). In addition to drought, environmental variables such as soil nutrient availability (Ewers et al., 2000) and soil texture (Hacke et al., 2000) have been shown to influence xylem vulnerability.

Xylem vulnerability has been reported to increase with conduit diameter both within species (Salleo and Logullo, 1989; Logullo and Salleo, 1993; Hargrave et al., 1994) and within individuals, where root xylem is usually more vulnerable than shoot xylem (Alder et al., 1996; Mencuccini and Comstock, 1997; Sperry and Ikeda, 1997). However, it has been proposed that vulnerability is not intrinsically related to conduit diameter (Tyree and Dixon, 1986; Sperry and Sullivan, 1992), but is instead determined by the permeability of the pit membrane to passage of the air/water interface during air seeding (Sperry and Tyree, 1990), which may be correlated with conduit size. 'Native' embolism representing up to a 20% loss of conductivity is usually present in tree stems (Tyree and Ewers, 1991). In general, species with a gradual cavitation response to decreasing pressure tolerate more native embolism than those with a rapid response (shallow versus steep sloped vulnerability curves) (Tyree and Ewers, 1991; Sperry, 1995). Jones and Sutherland (1991) predicted that cavitation was required in species with shallow sloped vulnerability curves before stomatal conductance could be maximized for a given soil water potential. Using a more advanced model, Sperry et al. (1996) predicted that at maximum rates of transpiration cavitation actually causes hydraulic conductance to approach zero at the limiting point in the pathway from soil to leaves.

The fine balance between normal xylem operating pressures and loss of hydraulic conductivity suggests a functional role for cavitation as part of a feedback mechanism linking stomatal regulation of transpiration to hydraulic conductance and plant water status (Jones and Sutherland, 1991; Sperry, 1995; Salleo et al., 2000). Stomatal conductance is typically coordinated with the leaf area-specific hydraulic conductance of the soil-to-leaf pathway (Küppers, 1984; Meinzer and Grantz, 1990; Meinzer et al., 1992, 1995). Saliendra et al. (1995) proposed that cavitation in *Betula occidentalis* Hook. was an adaptive mechanism that quickly reduced hydraulic conductance and transpiration as drought developed, thereby conserving soil water and optimizing stomatal conductance. Other experiments have demonstrated that water released from the lumens of xylem conduits by cavitation could act to buffer leaf water status over short time periods (Tyree and Dixon, 1983; Dixon et al., 1984; Tyree and Yang, 1990; Logullo and Salleo, 1992). However, a role for cavitation as a functional, dynamic form of capacitance was usually discounted because embolized conduits were considered repairable only over long time periods (Brough et al., 1986; Holbrook, 1995). Interaction between stomatal and hydraulic conductance was therefore seen as allowing a given level of embolism and loss of conductance to develop, and that this level would remain constant or change only gradually throughout the season (Magnani and Borghetti, 1995).

4.2. Recent advances and controversies

Recent studies have revealed that the rapid refilling of embolized conduits is common in both woody and herbaceous plants, even while tension is present in the xylem (Sobrado et al., 1992; Edwards et al., 1994). Salleo et al. (1996) demonstrated xylem refilling in *Laurus nobilis* L. stems within 20 min of induction of emboli using positive pressure. Refilling occurred while xylem pressure was below -1.0 MPa. Canny (1997a,b) snap froze *Helianthus* petioles to liquid nitrogen temperatures and observed vessel contents directly using a cryo-scanning electron microscope (CSEM). Up to 40% of vessels were embolized by 09:00 h, and the proportion of embolized vessels decreased throughout the day to reach low levels in the afternoon when xylem pressures were lowest and transpiration was highest. Similar patterns of daily embolism and refilling of root and stem xylem vessels have now been observed in a variety of crop and woody species using the same technique (McCully et al., 1998; McCully, 1999; Buchard et al., 1999; Melcher et al., 2001). Nevertheless, there is some controversy over the possibility that emboli are generated during freezing as an artifact of the cryo-freezing technique (Cochard et al., 2000), despite previous evidence to the contrary (Pate and Canny, 1999; McCully et al., 2000). Consistent with CSEM observations, xylem hydraulic conductivity also varied diurnally

in the petioles and woody twigs of coniferous and hardwood trees (Zwieniecki and Holbrook, 1998; Zwieniecki et al., 2000).

Fast refilling under tension would be difficult to reconcile with the existing paradigms of xylem water transport and embolism repair. For a gas bubble to dissolve into xylem sap that is already saturated with air, pressure inside the bubble must exceed atmospheric pressure. Dissolution occurs at a threshold xylem pressure determined by the surface tension, and hence radius, of the bubble. Xylem pressure in even relatively narrow conduits (< 20 μm in diameter) must rise to within -15 kPa before dissolution will begin (Tyree et al., 1999). Embolism repair was therefore thought to be limited to periods of high water availability and zero evaporative demand (Waring et al., 1979; Magnani and Borghetti, 1995), or to species that developed root pressure (Sperry et al., 1994; Fisher et al., 1997). Several previous examples of embolism repair in stem segments did conform to the physical laws governing the dissolution and diffusion of gas in the bubbles (Tyree and Yang, 1992; Yang and Tyree, 1992; Lewis et al., 1994), but in another example, afternoon repair was detected at much lower xylem pressures (Salleo and Logullo, 1989).

To determine how refilling under tension could occur, two problems must be addressed. First, how could water move into a refilling conduit against a gradient in pressure (from full vessels) or osmotic potential (from living xylem and phloem cells)? Secondly, how could a pressure that is high enough to dissolve emboli be maintained in a refilling conduit that is adjacent to full conduits at much lower pressures? In answer to the first problem, it has been proposed that refilling can occur through secretion of osmotica into embolized conduits by surrounding xylem parenchyma, with water moving into the conduits by osmosis (Grace, 1993). Solute concentrations are low in refilling xylem, and are not high enough to overcome pre-existing gradients in water potential (Tyree et al., 1999; McCully, 1999). The theory of compensating tissue pressure Canny (1995, 1998)stated that the entire vascular tissue was pressurized, with the dual effects of forcing water into embolized conduits (problem 1) and negating

tension in conducting vessels (problem 2). However, it is difficult or even impossible to account for the existence of such pressures operating at the scale of the entire vascular tissue, or to envisage counter flows of water into the swelling living tissue and the embolized conduits at same time (Comstock, 1999; Tyree et al., 1999). Holbrook and Zwieniecki (1999), in the most parsimonious explanation of embolism repair so far, proposed that water may be actively extruded into embolized conduits through membrane water channels (aquaporins), and that compartmentalization of repair is the result of xylem cell wall chemistry and bordered pit geometry. According to their theory, the non-zero contact angle of extruded, coalescing water droplets on the hydrophobic inner walls of the refilling conduit allows positive pressures to develop that are high enough to dissolve gas within the lumen, but not high enough to force the air/water interface across the bordered pit channel. The angle of the bordered pit chamber ensures that contact with neighboring conduits is not re-established until most of the gas in the embolized vessel is forced into solution (Holbrook and Zwieniecki, 1999). In support of their hypothesis, refilling was inhibited by phloem girdling and metabolic poisons (Zwieniecki et al., 2000). However, in an earlier study by Borghetti et al. (1991), metabolic poisons did not prevent refilling.

4.3. Conclusions and recommendations

The ability to repair cavitated xylem has important implications for understanding the regulation of tree water use. Hydraulic conductance can now be viewed as a dynamic balance between embolism formation and repair, and may vary continuously throughout the day in response to changes in plant water status and the vigor of the refilling mechanism (Holbrook and Zwieniecki, 1999). More effort and new techniques are now required to determine the actual mechanism of embolism removal, the role that living cells play in the process, and the significance of xylem cell wall chemistry and structure. Recent advances in the study of plant aquaporins may yield insights and techniques that can be applied to the study of

embolism repair (Tyerman et al., 1999). Surveys that document the prevalence of embolism repair are required, including comparisons between herbaceous plants and trees, hardwoods and conifers, and tree taxa of differing xylem anatomy and ecology. What is the relationship between embolism repair and more traditional measures of xylem vulnerability to cavitation? To what extent do vulnerability curves represent a balance between the physical process of air seeding and a vital process of embolism repair (Stiller and Sperry, 1999)? The first studies to clearly document diurnal embolism formation and repair highlight temporal variation in the rate of refilling. Why does embolism appear to be at its maximum in the morning when tensions are low, and refilling appear to be fastest in the afternoon when tensions are high? The answer to this question may lie in the role of cavitation as a potential source of stored water (discussed below).

5. Hydraulic architecture

Hydraulic architecture, the structure and properties of the transport system that govern the balance between efficiency of water supply and total transpiring leaf area (Zimmermann, 1978), is a major determinant of leaf water status and stomatal behavior. If hydraulic capacity is limiting, leaf and stem water potentials may be reduced to the point of xylem cavitation and embolism, resulting in stomatal closure and limitation of transpiration and photosynthesis. The temporal dynamics of the leaf water balance can also be affected by the exchange of water between internal storage compartments along the hydraulic pathway and the transpiration stream (Goldstein et al., 1984; Holbrook, 1995; Goldstein et al., 1998).

5.1. General patterns

Recent reviews by Tyree and Ewers (1991, 1996) provide a thorough description of the history, concepts and components of tree hydraulic architecture. In most trees, leaf-specific conductivity (k_l) decreases from the base of the stem to the

apex and from larger to smaller diameter stems (Zimmermann, 1978; Tyree et al., 1991; Joyce and Steiner, 1995). Exceptions occur in trees with strong apical control, where k_l may remain relatively constant or increase towards the dominant apex (Ewers and Zimmermann, 1984; Tyree and Ewers, 1996). In general, conduit diameter and k_s are highest in the roots, intermediate in the main stem and lowest in the most peripheral stems (Zimmermann, 1983; Gartner, 1995). The diameter of new conduits tends to increase as the main stem grows radially (Zimmermann, 1983; Mencuccini et al., 1997), such that the axial resistance of the main stem may be at least partially independent of the increasing path length as trees grow larger (West et al., 1999). Branches usually have narrower conduits, lower k_s and lower k_l when compared to the main stem at a similar size (Gartner, 1995). In some trees, the junction between higher and lower order branches is a site of reduced k_s and k_l, due either to decreased conduit diameter or the increased frequency of conduit ends (Zimmermann, 1978; Tyree and Alexander, 1993; Logullo et al., 1995).

The pattern of decreased k_l at branch junctions and gradually decreasing k_l towards peripheral organs led Zimmermann (1978, 1983) to propose the segmentation hypothesis: decreased conductivity causes steeper pressure gradients and an increased possibility of cavitation in peripheral organs for a given rate of transpiration. Cavitation and embolism blockage during drought should occur first in expendable twigs and leaves, thus reducing transpiration and protecting larger stems and roots. The segmentation hypothesis was later modified to include both hydraulic and vulnerability segmentation (Tyree et al., 1991, 1993a; Tsuda and Tyree, 1997). Hydraulic segmentation refers to lower k_l in higher order branches and branch junctions. However, if stomatal conductance and transpiration are reduced in response to water stress, gradients in water potential are also reduced and hydraulic segmentation may not be effective. Vulnerability segmentation occurs when the xylem of more distal organs is more vulnerable to cavitation, thus causing preferential loss of these parts during drought stress even if transpiration is reduced. Tsuda and Tyree (1997) demon-

strated that vulnerability segmentation occurs in *Acer saccharinum* L., a species with high overall hydraulic conductivity and vulnerability, and proposed a trade-off between hydraulic conductivity and vulnerability segmentation. Vulnerability segmentation may be more common in trees with high total plant conductance and only moderate gradients in water potential during transpiration. Hydraulic segmentation and low overall vulnerability may be more common in trees with low plant conductance, low rates of water use and steep gradients in water potential (Tsuda and Tyree, 1997). Another pattern, highest vulnerability and k_s in the roots, observed in *B. occidentalis*, was thought to be an adaptation to more mesic environments and high rates of water use (Tsuda and Tyree, 1997). However, continued research has now shown that maximum vulnerability in the roots is the norm rather than the exception, even in conifers and drought adapted angiosperms with low total conductance (Alder et al., 1996; Mencuccini and Comstock, 1997; Kavanagh et al., 1999).

5.2. Whole-plant hydraulic conductance

Measurements of hydraulic conductance on whole plants are more pertinent than branch or excised segment measurements for determining whole-tree transport sufficiency (Becker et al., 1999). To account for size effects and reveal functional differences in tree architecture, the hydraulic conductance of whole trees (K_p) and whole root (K_r) and shoot (K_s) systems can be expressed on a unit leaf area (e.g. $K_{p,la}$) or sapwood area (e.g. $K_{s,sa}$) basis. Division of K_r by root surface area can reveal differences in radial conductance and is therefore a measure of root efficiency, but is less useful for comparisons between trees with different functional characteristics (Tyree et al., 1998). Division of K_r by root dry mass or leaf surface area better reflects the efficiency of total investment in roots and adaptive differences in shade or drought tolerance (Tyree et al., 1998). In the past K_p has been estimated from measurements of water potential differences between the soil and leaves and whole-tree evaporative flux (the evaporative flux method; Hellkvist et al.,

1974; Meinzer et al., 1995). Such measurements are relevant to whole tree functioning and are mathematically simple (Yang and Tyree, 1993), but are prone to errors in measurement of transpiration and variation in leaf water potential within the crown. In addition it may be difficult to separate the contribution of roots and shoots to total resistance (where $R_p = 1/K_p$), and the release of stored water or increases in axial resistance caused by cavitation often cause diurnal variation in estimates of K_p (Granier et al., 1989; Irvine et al., 1998).

The introduction of the high-pressure flow meter (HPFM) has permitted the conductance of decapitated roots to be measured in situ, as well as the conductance of whole, excised shoots (Tyree et al., 1993b, 1994, 1995). Measurement of root conductance (K_r) is achieved by pushing water from the cut surface towards the root apex in the opposite direction to normal flow. This technique has the advantage that it is not necessary to remove the roots from the soil, but a hysteresis in the relationship between applied pressure and flow is usually observed, and is attributed to an increase in solute concentration within the roots caused by the reversal of normal flow (Tyree et al., 1994). Solute accumulation can be avoided and K_r measured accurately if the flow path is free of air bubbles and fast, 'transient', measurements of flow are made every few seconds while the pressure is quickly increased (see Magnani et al., (1996) for an alternative method). Using the HPFM, $1/K_p$ is found as the sum of $1/K_s$ and $1/K_r$, and the contribution of the separate components of the pathway, such as leaves and small twigs, can be found by repeated measurement of conductance after successive removal of the parts of interest (Zotz et al., 1998). Except for leaf and petiole resistances, good agreement was found between the HPFM and evaporative flux methods in the only direct comparison so far (Tsuda and Tyree, 1997). During measurement of shoot hydraulic resistance with the HPFM, water is forced into the leaf air spaces and drips from the stomata. Perfusion occurs slowly and stable flow rates are sometimes difficult to achieve, particularly with large shoots. Even when stable flow rates are achieved, water is flowing through spaces

that it would not normally occupy, probably leading to underestimates of leaf resistance because water under pressure will take the path of least resistance into the air spaces. Normal transpiration may be predominantly peristomatal and therefore involve a longer path in the liquid phase and higher resistance from the minor veins to the site of evaporation (Yang and Tyree, 1994). Caution is therefore warranted in the interpretation of measurements of K_s and leaf resistance obtained using the HPFM until further comparisons are made (Mencuccini and Magnani, 2000). It also should be recognized that because prolonged application of high pressure with the HPFM reverses embolism, the resulting maximum conductances may be greater than in situ conductances of water-stressed plants with substantial native embolism.

Measurements at the whole tree level have begun to reveal the adaptive significance of tree hydraulic architecture across taxa of sometimes-divergent growth forms. Forest gap-colonizing pioneer species from Panama had higher $K_{p,la}$ and higher root conductance on a root dry weight basis than more shade tolerant species (Tyree et al., 1998). Similarly, Becker et al. (1999) reported that fast-growing pioneer species of both tropical angiosperms and gymnosperms had consistently higher $K_{p,la}$ and $K_{p,sa}$ than late successional species. In contrast with earlier studies, similar transport sufficiency at the whole plant level was found among gymnosperms and angiosperms, even though measurements at the branch level confirmed previous reports of lower k_s and k_l in gymnosperms (Becker et al., 1999). It is possible that the lower k_s of gymnosperm wood was balanced by compensating differences in hydraulic and plant architecture, most likely in the roots and leaves (Becker et al., 1999).

Adaptive, differences in whole-plant hydraulic architecture have also been found for a range of Mediterranean *Quercus* species differing in drought tolerance. K_p was highest in species adapted to more mesic environments, and there was usually good correlation between K_r, K_s and conductance of the leaf blade (Nardini and Tyree, 1999). Within arid environments, drought-avoiding species maintained higher $K_{r,la}$ and leaf water

content throughout the dry periods, whereas drought tolerant species showed a decline in root conductance and leaf water content (Nardini et al., 1998; Nardini and Pitt, 1999; Nardini et al., 1999). In all of these examples it was concluded that high whole-plant conductance allows pioneer, mesic and drought avoiding species to maintain higher minimum leaf water potentials when water is abundant or only moderately limiting (Tyree et al., 1998). Based on similar results from Hawaiian dry forest species, Stratton et al. (2000b) concluded that simple classification into drought avoiding and drought tolerant groupings belies the underlying physiological convergence in plant–water relationships. The disparate behavior of each ecological grouping at the leaf level was instead related to a common functional relationship between physiological responses and aspects of plant hydraulic architecture.

Measurements at the whole tree level have also provided important information on the partitioning of resistance along the hydraulic pathway from soil to leaf. Within the roots and shoots, the contribution of the component parts to total resistance varies widely between taxa and environments, but usually the majority of resistance is located in the roots and narrow branches and leaves (Yang and Tyree, 1994). Larger diameter roots and stems occupy a smaller proportion of total resistance. Such observations are of direct relevance to the current debate surrounding the causes of decline in forest stand productivity with age. After reviewing a number of potential causes, Ryan and Yoder (1997) hypothesized that increases in axial resistance as trees grow larger and taller leads to hydraulic limitation of transpiration and photosynthesis and hence stand productivity and maximum tree height. Some evidence is available to support their contention that stomatal limitation of photosynthesis increases with tree height (Ryan et al., 1997; Hubbard et al., 1999; Bond and Ryan, 2000). However, Becker et al. (2000) argued that increases in length of the axial transport pathway would have less effect on total resistance if larger diameter stems and roots contribute only a minor proportion to total resistance. Sapwood porosity is also usually higher and leaf area/sapwood area lower in large trees

(Zimmermann, 1983), thus potentially mitigating against increases in resistance due to path-length. Nevertheless, Mencuccini and Magnani (2000) concluded that these compensatory changes in hydraulic architecture are not enough to prevent above ground hydraulic resistance from increasing with tree height. They instead propose that increases in allocation to fine roots may compensate for the increased contribution of stems to total hydraulic resistance with size, but that such changes must involve a carbon cost that contributes to a decline in productivity with size (Magnani et al., 2000). Tests of the hydraulic limitation hypothesis need to unambiguously quantify any changes that occur in the partitioning of total resistance between the various parts of the soil-to-leaf pathway during tree growth, and in particular should address the contribution of roots and leaves to hydraulic resistance (Mencuccini and Magnani, 2000). Regardless of the properties of the hydraulic pathway, gravity is expected to diminish the driving force for water movement by 0.1 MPa for every 10-m increase in height.

5.3. Storage, cavitation and hydraulic signaling

In addition to acting as the pathway for water transport, tree roots and stems act as storage compartments for water. If transpiration increases and water potential drops, water moves from storage into the transpiration stream, helping to minimize temporal imbalances between water supply and demand and temporarily slowing the decline in leaf water potential (Holbrook, 1995). The larger the tree, the greater the storage capacity and the longer the time lag between the onset of transpiration from the crown and sap flow at the base of the tree (Goldstein et al., 1998). Increasing storage capacity as trees grow larger may partially compensate for increases in axial resistance with tree height (Goldstein et al., 1998). $K_{p,la}$ measured using the evaporative flux method can vary continuously throughout the day as storage compartments are drained and recharged, hence the use of the term 'apparent' hydraulic conductance (Andrade et al., 1998; Meinzer et al., 1999b).

Despite the importance of stem water storage in regulating the water economy of plants, limited information exists on the contribution of internal water storage to their total daily water consumption. Some studies of internal water storage capacity have focused on the total amount of available water in a particular tissue compartment in relation to total transpiring leaf area (Goldstein et al., 1984; Meinzer and Goldstein, 1986). More recently, and as a consequence of development of simple, robust technology for monitoring sap flow in intact stems, the mass of water that can be withdrawn from the main stem and branches during the day and replaced over a 24 h cycle, has been used to assess the diurnal water storage capacity (e.g. Goldstein et al., 1998). If the total amount of water that is withdrawn from the storage compartment and used in replenishing the water lost by transpiration is not known, then the intrinsic water storage capacity can be estimated as the amount of water that can be withdrawn for a given change in water potential of the storage compartment. This change in water content per unit change in water potential is generally referred to as the tissue's capacitance (Jarvis, 1975; Tyree and Jarvis, 1982).

Nearly all woody plants contain tissues within or associated with the water transport pathway, particularly the sapwood that could function in water storage. Living cells of the sapwood with elastic walls, which can undergo substantial changes in volume with relatively small changes in turgor, are well suited as intracellular water storage elements. Extracellular water stores include water retained within intercellular spaces and the lumens of cavitated xylem elements (Tyree and Yang, 1990). Although sapwood has diffuse boundaries with adjacent tissues and may function both in storage and conduction, parenchymatous tissues such as the pith and/or associated bark tissues in stems of some woody plants, have clearly defined boundaries, and only serve, with few exceptions, as internal water reservoirs (Goldstein et al., 1984; Franco-Vizcaino et al., 1990; Nilsen et al., 1990; Holbrook and Sinclair, 1992a,b). These elastic parenchymatous tissues whose function appears to be mainly water storage have the disadvantage of being at some dis-

tance from the main vascular conduits. In order to serve effectively as a water reservoir in trees, these tissues have to be in relatively close contact and have good hydraulic connections with the sapwood. These functional constraints may have prevented elastic stem tissues from developing into more conspicuous water storage compartments in large trees.

Water stored in stem tissues can contribute from 6 to 50% of the total water loss by transpiration during a 24-h cycle (Tyree and Yang, 1990; Schulze et al., 1985; Waring and Running, 1978; Waring et al., 1979; Goldstein et al. 1998). The contribution of internal water storage to daily transpirational losses is not a fixed parameter in the water budget of trees. For example, the amount of water stored in the trunk of *Pinus pinaster* Aiton. accounted for 12% of the daily transpiration when soil water was abundant, but increased to 25% at the end of summer following a period of drought (Loustau et al., 1996). Even if the absolute amount of water obtained from internal storage during a day is relatively small, its role in the maintenance of a favorable leaf water and carbon balance may be significant (Logullo and Salleo, 1992; Goldstein et al., 1998).

Most discussions of water storage in trees have discounted the contribution of water from cavitation of functional conduits because this would provide only a temporary improvement in leaf water status at the expense of a presumably permanent loss of hydraulic function (Holbrook, 1995). If emboli can be quickly removed in many taxa as recent reports suggest (Zwieniecki and Holbrook, 1998; Tyree et al., 1999; Melcher et al., 2001), cavitation is likely to be more important as a source of stored water than previously thought. Xylem conduits may have dual purpose as both conducting and storage compartments (Phillips et al., 1997; Fruh and Kurth, 1999). Diurnal variation in $K_{p,la}$ can be at least partly attributed to the dynamic cavitation and repair process (Zwieniecki et al., 2000), rather than the release and recharge of water from permanently embolized conduits, and fibers and xylem parenchyma (Holbrook, 1995). Differences between conifers and hardwoods in their reliance on stored water might be related to differences in their capacity for embolism repair (Holbrook, 1995).

Hydraulic function and leaf physiology are linked through the effect of 'hydraulic signals' on stomatal regulation of transpiration. Partial removal or covering of tree foliage usually induces a rapid increase in stomatal conductance in the remaining foliage (Meinzer and Grantz, 1990; Whitehead et al., 1996; Pataki et al., 1998). The stomata are thought to respond to some form of hydraulic signal, generated by the perturbation of the hydraulic pathway, even though bulk leaf water potential may remain relatively constant during the change (Whitehead et al., 1996; Whitehead 1998). Salleo et al. (2000) recently proposed that stomatal closure in response to cavitation is also the result of a hydraulic signal generated by the onset of cavitation itself. What is the nature of the hydraulic signal and how is it sensed? Defoliation and covering transiently increase leaf-specific hydraulic capacity, whereas cavitation and treatments such as stem wounding decrease hydraulic capacity. Is the same hydraulic control mechanism operating in both cases? There is general agreement that the mechanism is not a simple negative feedback response to bulk leaf water potential, but it may be a threshold response to a critical level of water potential that triggers cavitation in the leaf or nearby stem xylem (Saliendra et al., 1995; Bond and Kavanagh, 1999; Salleo et al., 2000). Cavitation causes a transient release of water that can buffer leaf water status (Dixon et al., 1984; Logullo and Salleo, 1992), but it also causes a decline in hydraulic conductivity. Are stomata responding to local changes in gradients of water potential between the leaf xylem and mesophyll or epidermal tissues that are not detected when using the pressure chamber to measure leaf water potential (Sperry, 1995; Buckley and Mott, 2000)? Chemical signals might also be involved, released by xylem parenchyma at the site of cavitation or somewhere in the leaf in response to changes in the water potential gradients (Whitehead et al., 1996; Salleo et al., 2000). Future studies of the effect of hydraulic perturbations on stomatal function require improved techniques for the measurement of water potential within the stem and leaves.

6. Trees as whole organisms

Because of their large size and logistical difficulties in gaining access to their crowns, the understandable tendency has been to study water transport in trees at a single scale or over a limited range of scale. However, this has contributed to a strong emphasis on differences rather than similarities among species in regulation of whole-tree water transport. Certainly, substantial differences among tree species in stomatal regulation of water use at the leaf level have been demonstrated. Nevertheless, it is of considerable interest to understand how whole-plant architectural, structural and physiological properties upstream contribute to the stomata in the terminal portion of the water transport pathway behaving as they do. Because trees are large, integrated organisms rather than mere collections of individual leaves conveniently displayed for enclosing in gas exchange chambers, it is relevant to examine the extent to which different species exhibit functional convergence with regard to regulation of their water economy at the whole-tree and intermediate scales. Although tree architecture may result in individual branches exhibiting a marked degree of physiological autonomy (Sprugel et al., 1991), striking similarities in behavior may be revealed when appropriate normalizing and scaling factors are identified.

Convergence in functioning among phylogenetically diverse animal species has been known for a long time. A few classic examples from animal studies include the dependence of metabolic rate and lifespan on body size (Calder, 1984; Schmidt-Nielsen, 1984). These relationships often conform with a power function of the form $Y = Y_0 M^b$ where Y is the process or characteristic of interest, M is mass, b is the power exponent, and Y_0 is a normalization constant whose value depends on the feature and kind of organism being studied. Explicit analyses of the influence of body size on structure–function relationships in trees and other plants have been largely lacking. Recently, however, quarter-power universal allometric scaling models describing the dependence of variables such as water use and population density on plant size have been proposed (Enquist et al., 1998;

West et al., 1999). Although studies specifically designed to test these models have yet to be conducted, a substantial amount of empirical data in the literature appear to be consistent with them. For example, Enquist et al. (1998) found that total daily water use among 37 plant species scaled with stem diameter in a similar manner. When stem diameter was converted to aboveground dry mass using relationships available in the literature, total daily water use was essentially proportional to the 3/4 power of mass. In a recent study of water use characteristics in more than 20 phylogenetically diverse co-occurring tropical forest tree species, a common relationship between sapwood cross-sectional area and stem diameter was observed (Meinzer et al., 2001). Conversion of stem diameter to aboveground dry mass (M) resulted in sapwood area scaling as $M^{0.74}$. Consistent with the shared allometric relationship between sapwood area and tree size, a common relationship between sap flow and tree size was also observed (Meinzer et al., 2001). At first sight it may seem counterintuitive that features such as sapwood cross-sectional area and sap flow should scale similarly with plant size in species as ecologically disparate as a boreal forest conifer and a tropical rainforest angiosperm. Nevertheless, existing data suggest substantial convergence in allometric relationships among ecologically and phylogenetically diverse species (Table 1, Fig. 3). At a smaller scale, however, known patterns of sap velocity, pressure gradients and leaf-specific conductance within trees do not appear to be consistent with some of the predictions of the model of West et al. (1999).

Despite the relatively large number of published studies on sapwood area and sap flow in trees (Wullschleger et al., 1998), there is still insufficient information to determine whether the dependence of sapwood area and sap flow on tree size is essentially universal for temperate and tropical angiosperm and gymnosperm trees. The extent to which variation in published sapwood area–tree size relationships among and within species is attributable to the use of different criteria to assess sapwood area is not known. For example, wood appearance alone has been used to assess functional xylem depth in some studies, whereas

Table 1
Species used to plot sapwood area–DBH relationship shown in Fig. 3

Species	Family	Location	Symbol in Fig. 3	Reference
Abies balsamea (L.) Mill.	Pinaceae	Maine	Ab	Gilmore et al., 1996
Acacia dealbata Link.	Fabaceae	Australia	Ad	Vertessy et al., 1995
Anacardium excelsum (Bert. & Balb.)	Anacardiaceae	Panama	Ae	Meinzer et al., 2001[a]
Carapa procera DC.	Meliaceae	French Guiana	Cp	Granier et al., 1996
Eucalyptus grandis Hill ex Maiden	Myrtaceae	Australia	Eg	Dye et al., 1992
Eucalyptus regnans F. Muell.	Myrtaceae	Australia	Er	Vertessy et al., 1995
Ficus insipida Willd.	Moraceae	Panama	Fi	Meinzer et al., 2001[a]
Hirtella glandulosa Spreng.	Chrysobalanaceae	French Guiana	Hg	Granier et al., 1996
Lecythis idatimon Aubl.	Lecythidaceae	French Guiana	Li	Granier et al., 1996
Miconia ferruginata DC.	Melastomataceae	Brazil	Mf	Meinzer et al., 2001[a]
Picea abies (L.) Karst	Pinaceae	Estonia	Pa	Sellin, 1994
Pinus pinaster Aiton.	Pinaceae	Portugal	Pp	Loustau et al., 1996
Pinus radiata D. Don.	Pinaceae	Australia	Pr	Teskey and Sheriff, 1996
Pinus sylvestris L.	Pinaceae	Scotland	Ps	Mencuccini and Grace, 1995
Populus fremontii S. Wats.	Salicaceae	Arizona	Pf	Schaeffer and Williams, 1998
Salix goodingii Ball.	Salicaceae	Arizona	Sg	Schaeffer and Williams, 1998
Tachigalia versicolor Standl. & L.O. Wms.	Fabaceae	Panama	Tv	Meinzer et al., 2001[a]

[a] Unpublished observations.

more quantitative criteria such as dye travel and measurements of sap flow at different depths in the stem have been employed in other studies. Confirmation of the universality of scaling of plant vascular systems and water use (Enquist et al., 1998; West et al., 1999) awaits the use of comparable methods to assess these relationships in a broader range of species.

As stated above, traditional reliance on leaf area-based measurements to compare stomatal regulation of transpiration among species often reveals a wide range of behavior. Nevertheless, in the absence of additional information, it is difficult to determine whether the patterns observed reflect intrinsic differences in the physiological responsiveness of components of the stomatal regulatory system, or whether they are attributable to other species- or size-specific features that cause the regulatory system to operate over different ranges along a common physiological response curve, or surface in the case of two interacting variables. The so-called stomatal re-

sponse to humidity provides an example of apparently divergent regulatory behavior that can converge when appropriate reference points and normalizing factors are taken into account. Bunce
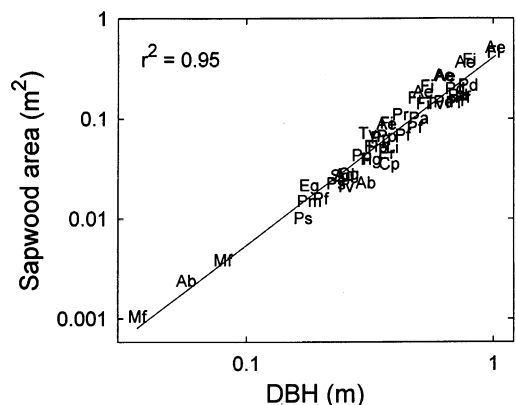

Fig. 3. Sapwood area in relation to DBH for 18 gymnosperm and angiosperm tree species growing in a range of temperate and tropical sites. Symbols are defined in Table 1. Note that data are plotted on log scales.
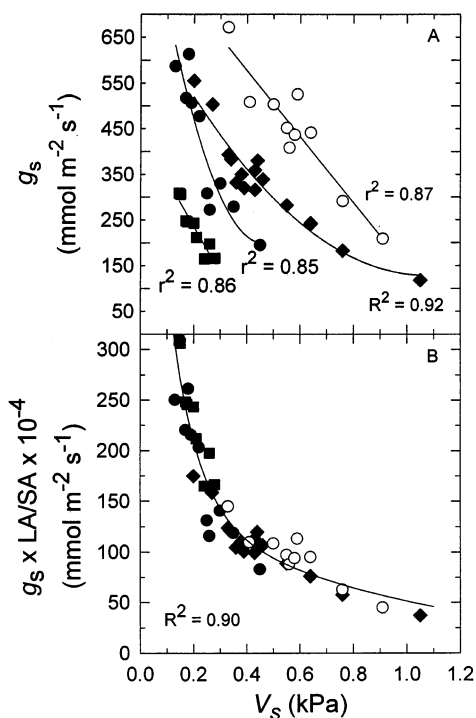
Fig. 4. (A) Stomatal conductance (g_s); and (B) g_s normalized by branch leaf area/sapwood area ratio (LA/SA) in relation to leaf-to-air vapor pressure difference referenced to the leaf surface (V_s) for four Panamanian forest tree species. Symbols: ◆, *Cecropia longipes*; ○, *Ficus insipida*; ●, *Luehea seemannii*; ■, *Spondias mombin*. Adapted from Meinzer et al. (1997).

(1985) noted that apparent stomatal responsiveness to changes in bulk air humidity was influenced by leaf boundary layer conductance. When the leaf-to-air humidity difference was referenced to the leaf surface, stomatal responsiveness to increasing evaporative demand was similar. In contrast, Meinzer et al. (1997) observed dissimilar stomatal responses to increasing evaporative demand among four tropical forest canopy tree species even when the leaf-to-air humidity difference was referenced to the leaf surface (Fig. 4(A)). However, when stomatal conductance was normalized by the leaf area:sapwood area ratio for the branches on which it was measured, the responses of conductance to increasing evaporative demand converged (Fig. 4(B)). These results imply that at a given combination of leaf area:sapwood area ratio and evaporative demand scaled to com-

parable reference points, transpiration rates on a leaf area basis would have been identical in the four contrasting species studied. These results further suggest that apparent intrinsic differences in stomatal regulatory behavior may actually represent stomatal sensing of different ranges of evaporative demand and liquid water transport capacity relative to capacity for water vapor loss (leaf area:sapwood area ratio).

The preceding considerations point to some of the pitfalls involved in relying on measurements at a single scale to characterize regulation of water transport in trees. Fortunately, improved access to entire trees via towers and cranes has made it logistically less daunting to study water transport over a range of scale spanning the single leaf to the entire tree. Simultaneous measurements at multiple scales will facilitate detection of convergence in functioning and will allow differences in stomatal behavior to be partitioned among intrinsic differences in physiological responsiveness to environmental variables and the influence of external factors associated with tree size and architecture.

Acknowledgements

References

Alder, N.N., Pockman, W.T., Sperry, J.S., Nuismer, S., 1997. Use of centrifugal force in the study of xylem cavitation. J. Exp. Bot. 48, 665–674.

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.

Allison, G.B., 1982. The relationship between [18]O and deuterium in water in sand columns undergoing evaporation. J. Hydrol. 55, 163–169.

Allison, G.B., Hughes, M.H., 1983. The use of natural tracers as indicators of soil water movement in a temperate semi-arid region. J. Hydrol. 60, 157–173.

Amin, M., 1982. Ascent of sap in plants by means of electrical double layers. J. Biol. Phys. 10, 103–109.

Andrade, J.L., Meinzer, F.C., Goldstein, G., Holbrook, N.M., Cavelier, J., Jackson, P., Silvera, K., 1998. Regulation of water flux through trunks, branches and leaves in trees of a lowland tropical forest. Oecologia 115, 463–471.

Balling, A., Zimmermann, U., 1990. Comparative measurements of the xylem pressure of Nicotiana plants by means of the pressure bomb and pressure probe. Planta 182, 325–338.

Becker, P., Meinzer, F.C., Wullschleger, S.D., 2000. Hydraulic limitation of tree height: a critique. Funct. Ecol. 14, 4–11.

Becker, P., Tyree, M.T., Tsuda, M., 1999. Hydraulic conductances of angiosperms versus conifers: similar transport sufficiency at the whole-plant level. Tree Physiol. 19, 445–452.

Begg, J.E., Turner, N.C., 1970. Water potential gradients in field tobacco. Plant Physiol. 46, 343–346.

Benkert, R., Balling, A., Zimmermann, U., 1991. Direct measurements of the pressure and flow in xylem vessels of Nicotiana tabacum and their dependence on flow resistance and transpiration rate. Bot. Acta 104, 423–432.

Benkert, R., Zhu, J.J., Zimmermann, G., Türk, R., Bentrup, F.W., Zimmermann, U., 1995. Long-term xylem pressure measurements in the liana Tetrastigma voinerianum by means of the xylem pressure probe. Planta 196, 804–813.

Bond, B.J., Kavanagh, K.L., 1999. Stomatal behavior of four woody species in relation to leaf-specific hydraulic conductance and threshold water potential. Tree Physiol. 19, 503–510.

Bond, B.J., Ryan, M.G., 2000. Comment on 'Hydraulic limitation of tree height: a critique' by Becker, Meinzer and Wullschleger. Funct. Ecol. 14, 137–140.

Borghetti, M., Edwards, W.R.N., Grace, J., Jarvis, P.G., Raschi, A., 1991. The refilling of embolized xylem in Pinus sylvestris L. Plant Cell Environ. 14, 357–369.

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. IAWA Bull. 5, 275–294.

Brough, D.W., Jones, H.G., Grace, J., 1986. Diurnal changes in water content of the stems of apple trees, as influenced by irrigation. Plant Cell Environ. 9, 1–7.

Buchard, C., McCully, M.E., Canny, M., 1999. Daily embolism and refilling of root xylem vessels in three dicotyledonous crop plants. Agronomie 19, 97–106.

Buckley, T.N., Mott, K.A., 2000. Stomatal responses to non-local changes in PFD: evidence for long-distance hydraulic interactions. Plant Cell Environ. 23, 301–309.

Bunce, J., 1985. The effect of boundary layer conductance on the stomatal response to humidity. Plant Cell Environ. 8, 55–57.

Burgess, S.S.O., Adams, M.A., Turner, N.C., Ong, C.K., 1998. The redistribution of soil water by tree root systems. Oecologia 115, 306–311.

Calder III, W.A., 1984. Size, Function and Life History. Harvard University Press, Cambridge, MA.

Caldwell, M.M., Richards, J.H., 1989. Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. Oecologia 79, 1–5.

Caldwell, M.M., Dawson, T.E., Richards, J.H., 1998. Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113, 151–161.

Canny, M.J., 1995. A new theory for the ascent of sap-cohesion supported by tissue pressure. Ann. Bot. 75, 343–357.

Canny, M.J., 1997a. Vessel contents during transpiration-embolisms and refilling. Am. J. Bot. 84, 1223–1230.

Canny, M.J., 1997b. Vessel contents of leaves after excision — a test of Scholander's assumption. Am. J. Bot. 84, 1217–1222.

Canny, M.J., 1998. Applications of the compensating pressure theory of water transport. Am. J. Bot. 85, 897–909.

Cochard, H., Bodet, C., Ameglio, T., Cruiziat, P., 2000. Cryo-scanning electron microscopy observations of vessel content during transpiration in walnut petioles. Fact or artifact? Plant Physiol. 124, 1191–1202.

Cochard, H., Cruiziat, P., Tyree, M.T., 1992. Use of positive pressures to establish vulnerability curves — further support for the air-seeding hypothesis and implications for pressure-volume analysis. Plant Physiology 100, 205–209.

Comstock, J.P., 1999. Why Canny's theory doesn't hold water. Am. J. Bot. 86, 1077–1081.

Connor, D.J., Legge, N.J., Turner, N.C., 1977. Water relations of mountain ash (Eucalyptus regnans R. Muell.) forests. Aust. J. Plant Physiol. 4, 753–762.

Corak, S.J., Blevins, D.G., Pallardy, S.G., 1987. Water transfer in an alfalfa.maize association. Plant Physiol. 84, 582–586.

Dawson, T.E., 1993. Hydraulic lift and water use by plants: implications for water balance, performance and plant–plant interactions. Oecologia 95, 565–574.

Dawson, T.E., 1996. Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the roles of tree size and hydraulic lift. Tree Physiol. 16, 263–272.

Dawson, T.E., Ehleringer, J.R., 1991. Streamside trees that do not use stream water. Nature 350, 335–337.

Dawson, T.E., Pate, J.S., 1996. Seasonal water uptake and movement in root systems of Australian phraeatophytic plants of dimorphic root morphology: a stable isotope investigation. Oecologia 107, 13–20.

Dixon, H.H., Joly, J., 1894. On the ascent of sap. Phil. Trans. R. Soc. Lond. B 186, 576.

Dixon, M.A., Grace, J., Tyree, M.T., 1984. Concurrent measurements of stem density, leaf and stem water potential, stomatal conductance and cavitation on a sapling of Thuja occidentalis l. Plant Cell Environ. 7, 615–618.

Dye, P.J., Olbrich, B.W., Calder, I.R., 1992. A comparison of the heat pulse method and deuterium tracing method for measuring transpiration from Eucalyptus grandis trees. J. Exp. Bot. 43, 337–343.

Edwards, W.R.N., Jarvis, P.G., Grace, J., Moncrieff, J.B., 1994. Reversing cavitation in tracheids of Pinus sylvestris L. under negative water potentials. Plant Cell Environ. 17, 389–397.

Ehleringer, J.R., Dawson, T.E., 1992. Water uptake by plants: perspectives from stable isotopes. Plant Cell Environ. 15, 1073–1082.

Enquist, B.J., Brown, J.H., West, G.B., 1998. Allometric scaling of plant energetics and population density. Nature 395, 163–165.

Ewers, B.E., Oren, R., Sperry, J.S., 2000. Influence of nutrient versus water supply on hydraulic architecture and water balance in *Pinus taeda*. Plant Cell Environ. 23, 1055–1066.

Ewers, F.W., Zimmermann, M.H., 1984. The hydraulic architecture of balsam fir (*Abies-balsamea*). Physiol. Plant 60, 453–458.

Fisher, J.B., Angeles, G., Ewers, F.W., Lopez-Portillo, J., 1997. Survey of root pressure in tropical vines and woody species. Int. J. Plant Sci. 158, 44–50.

Franco-Vizcaino, E., Goldstein, G., Ting, I.P., 1990. Comparative gas exchange of leaves and bark in three stem succulents of Baja, California. Am. J. Bot. 77, 1272–1278.

Fruh, T., Kurth, W., 1999. The hydraulic system of trees: Theoretical framework and numerical simulation. J. Theor. Biol. 201, 251–270.

Gartner, B.L., 1995. Patterns of xylem variation within a tree and their hydraulic and mechanical consequences. In: Gartner, B.L. (Ed.), Plant stems: physiological and functional morphology. Academic Press, San Diego, pp. 125–149.

Gilmore, D.W., Seymour, R.S., Maguire, D.A., 1996. Foliage–sapwood area relationships for *Abies balsamea* in central Maine. Can. J. For. Res. 26, 2071–2079.

Goldstein, G., Meinzer, F., Monasterio, M., 1984. The role of capacitance in the water balance of Andean giant rosette species. Plant Cell Environ. 7, 179–186.

Goldstein, G., Andrade, J.L., Meinzer, F.C., Holbrook, N.M., Cavelier, J., Jackson, P., Celis, A., 1998. Stem water storage and diurnal patterns of water use in tropical forest canopy trees. Plant Cell Environ. 21, 397–406.

Goldstein, G., Sarmiento G., 1986. Water relations of trees and grasses and their consequences for the structure of savanna vegetation. In: Waler, B. (Ed.), Determinants of tropical Savannas. Proceedings of the IUBS/SCZ workshop, Harare, Zimbabwe. IUBS Monograph Series No. 3, IRL Press, Oxford, pp. 13–38

Grace, J., 1993. Refilling of embolized xylem. In: Borghetti, M., J. Grace, Raschi, A. (Eds.), Water transport in plants under climate stress. Cambridge University Press, Cambridge, pp. 51–62.

Granier, A., Breda, N., Claustres, J.P., Colin, F., 1989. Variation of hydraulic conductance of some adult conifers under natural conditions. Ann. Sci. For. 46, S357–S360.

Granier, A., Huc, R., Barigah, S.T., 1996. Transpiration of natural rain forest and its dependence on climatic factors. Agric. For. Meteorol. 78, 19–29.

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

Hales, S., 1727. Vegetable Staticks. W & J Inneys and T Woodward, London.

Hargrave, K.R., Kolb, K.J., Ewers, F.W., Davis, S.D., 1994. Conduit diameter and drought-induced embolism in *Salvia-Mellifera* Greene (labiatae). New Phytol. 126, 695–705.

Hellkvist, J., Richards, G.P., Jarvis, P.G., 1974. Vertical gradients of water potential and tissue water relations in Sitka spruce trees measured with the pressure chamber. J. Appl. Ecol. 11, 637–667.

Hinckley T.M., Richter H., Schulte P.J., 1991. Water relations. In: Raghavendra, A.S. (Ed.), Physiology of trees. Wiley, New York, pp. 137–162

Holbrook, N.M., 1995. Stem water storage. In: Gartner, B.L. (Ed.), Plant stems: physiological and functional morphology. Academic Press, San Diego, pp. 151–174.

Holbrook, N.M., Sinclair, T.R., 1992a. Water balance in the arborescent palm, *Sabal palmetto*. I. Stem structure, tissue water release properties and leaf epidermal conductance. Plant Cell Environ. 15, 393–399.

Holbrook, N.M., Sinclair, T.R., 1992b. Water balance in the arborescent palm, *Sabal palmetto* II. Transpiration and stem water storage. Plant Cell Environ. 15, 401–409.

Holbrook, N.M., Zwieniecki, M.A., 1999. Embolism repair and xylem tension: Do we need a miracle? Plant Physiol. 120, 7–10.

Hubbard, R.M., Bond, B.J., Ryan, M.G., 1999. Evidence that hydraulic conductance limits photosynthesis in old Pinus ponderosa trees. Tree Physiol. 19, 165–172.

Irvine, J., Perks, M.P., Magnani, F., Grace, J., 1998. The response of *Pinus sylvestris* to drought: stomatal control of transpiration and hydraulic conductance. Tree Physiol. 18, 393–402.

Jackson, P.C., Cavelier, J., Goldstein, G., Meinzer, F.C., Holbrook, N.M., 1995. Partitioning of water resources among plants of a lowland tropical forest. Oecologia 101, 197–203.

Jackson, P.C., Meinzer, F.C., Bustamante, M., Goldstein, G., Franco, A., Rundel, P.W., Caldas, L., Igler, E., Causin, F., 1999. Partitioning of soil water among tree species in a Brazilian Cerrado ecosystem. Tree Physiol. 19, 717–724.

Jackson, R.B., Sperry, J.S., Dawson, T.E., 2000. Root water uptake and transport: using physiological processes in global predictions. Trends Plant Sci. 5, 482–488.

Janes, B.E., Gee, G.W., 1973. Changes in transpiration, net carbon dioxide assimilation and leaf water potential resulting from application of hydrostatic pressure to roots of intact pepper plants. Physiol. Plant 28, 201–208.

Jarvis, P.G., 1975. Water transfer in plants. In: deVries, D.A., van Alfen, N.K. (Eds.), Heat and Mass Transfer in the Environment of Vegetation. Scripta Books, Washington DC, pp. 369–394.

Jones, H.G., Sutherland, R.A., 1991. Stomatal control of xylem embolism. Plant Cell Environ. 14, 607–612.

Joyce, B.J., Steiner, K.C., 1995. Systematic variation in xylem hydraulic capacity within the crown of white ash (*Fraxinus americana*). Tree Physiol. 15, 649–656.

Kavanagh, K.L., Bond, B.J., Aitken, S.N., Gartner, B.L., Knowe, S., 1999. Shoot and root vulnerability to xylem

cavitation in four populations of Douglas-fir seedlings. Tree Physiol. 19, 31–37.

Koch, G.W., Amthor, J.S., Goulden, M.L., 1994. Diurnal patterns of leaf photosynthesis, conductance and water potential at the top of a lowland rain forest canopy in Cameroon: measurements from the Radeau des Cimes. Tree Physiol. 14, 347–360.

Küppers, M., 1984. Carbon relations and competition between woody species in a Central European hedgerow. II. Stomatal responses, water use, and hydraulic conductivity in the root/leaf pathway. Oecologia 64, 344–354.

Le Roux, X., Bariac, T., Mariotti, A., 1995. Spatial partitioning of the soil water resource between grass and shrub components in a West African humid savanna. Oecologia 104, 147–155.

Lewis, A.M., Harnden, V.D., Tyree, M.T., 1994. Collapse of water-stress emboli in the tracheids of Thuja occidentalis L. Plant Physiol. 106, 1639–1646.

Logullo, M.A., Salleo, S., 1992. Water storage in the wood and xylem cavitation in 1-year-old twigs of Populus deltoides Bartr. Plant Cell Environ. 15, 431–438.

Logullo, M.A., Salleo, S., 1993. Different vulnerabilities of Quercus ilex L. to freeze-induced and summer drought-induced xylem embolism — an ecological interpretation. Plant Cell Environ. 16, 511–519.

Logullo, M.A., Salleo, S., Piaceri, E.C., Rosso, R., 1995. Relations between vulnerability to xylem embolism and xylem conduit dimensions in young trees of Quercus cerris. Plant Cell Environ. 18, 661–669.

Loustau, D., Berbiger, P., Roumagnac, P., Arruda-Pacheco, C., David, J.S., Ferreira, M.I., Pereira, J.S., Tavares, R., 1996. Transpiration of a 64-year-old maritime pine stand in Portugal. I. Seasonal course of water flux through maritime pine. Oecologia 107, 33–42.

Magnani, F., Borghetti, M., 1995. Interpretation of seasonal-changes of xylem embolism and plant hydraulic resistance in Fagus sylvatica. Plant Cell Environ. 18, 689–696.

Magnani, F., Centritto, M., Grace, J., 1996. Measurement of apoplasmic and cell-to-cell components of root hydraulic conductance by a pressure-clamp technique. Planta 199, 296–306.

Magnani, F., Mencuccini, M., Grace, J., 2000. Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. Plant Cell Environ. 23, 251–263.

McCully, M.E., 1999. Root xylem embolisms and refilling. Relation to water potentials of soil, roots, and leaves, and osmotic potentials of root xylem sap. Plant Physiol. 119, 1001–1008.

McCully, M.E., Huang, C.X., Ling, L.E.C., 1998. Daily embolism and refilling of xylem vessels in the roots of field-grown maize. New Phytol. 138, 327–342.

McCully, M.E., Baker, A.N., Shane, M.W., Huang, C.X., Ling, L.E.C., Canny, M.J., 2000. The reliability of cryoSEM for the observation and quantification of xylem embolisms and quantitative analysis of xylem sap in situ. J. Microsc. 198, 24–33.

McCutchan, H., Shackel, K.A., 1992. Stem–water potential as a sensitive indicator of water stress in prune trees (Prunus domestica L. cv. French). J. Am. Soc. Hort. Sci. 117, 607–610.

Meinzer, F.C., Goldstein, G., 1986. Adaptations for water and thermal balance in Andean giant rosette plants. In: Givnish, T. (Ed.), On the Economy of Plant Form and Function. Cambridge University Press, Cambridge, pp. 381–411.

Meinzer, F.C., Grantz, D.A., 1990. Stomatal and hydraulic conductance in growing sugarcane-stomatal adjustment to water transport capacity. Plant Cell Environ. 13, 383–388.

Meinzer, F.C., Goldstein, G., Andrade, J.L., 2001. Regulation of water flux through tropical forest canopy trees: Do universal rules apply? Tree Physiol. 21, 19–26.

Meinzer, F.C., Goldstein, G., Neufeld, H.S., Grantz, D.A., Crisosto, G.M., 1992. Hydraulic architecture of sugarcane in relation to patterns of water-use during plant development. Plant Cell Environ. 15, 471–477.

Meinzer, F.C., Andrade, J.L., Goldstein, G., Holbrook, N.M., Cavelier, J., Jackson, P., 1997. Control of transpiration from the upper canopy of a tropical forest: the role of stomatal, boundary layer and hydraulic architecture components. Plant Cell Environ. 20, 1242–1252.

Meinzer, F.C., Andrade, J.L., Goldstein, G., Holbrook, N.M., Cavelier, J., Wright, S.J., 1999a. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. Oecologia 121, 293–301.

Meinzer, F.C., Goldstein, G., Jackson, P., Holbrook, N.M., Gutierrez, M.V., Cavelier, J., 1995. Environmental and physiological regulation of transpiration in tropical forest gap species-the influence of boundary-layer and hydraulic-properties. Oecologia 101, 514–522.

Meinzer, F.C., Goldstein, G., Franco, A.C., Bustamante, M., Igler, E., Jackson, P., Caldas, L., Rundel, P.W., 1999b. Atmospheric and hydraulic limitations on transpiration in Brazilian cerrado woody species. Funct. Ecol. 13, 273–282.

Melcher, P.J., Meinzer, F.C., Yount, D.E., Goldstein, G., Zimmermann, U., 1998. Comparative measurements of xylem pressure in transpiring and non-transpiring leaves by means of the pressure chamber and the xylem pressure probe. J. Exp. Bot. 49, 1757–1760.

Melcher, P.J., Goldstein, G., Meinzer, F.C., Yount, D., Jones, T., Holbrook, N.M., Huang, C.X., 2001. Water relations of coastal and estuarine Rhizophora mangle: Xylem tension and dynamics of embolism formation and repair. Oecologia 126, 182–192.

Mencuccini, M., Comstock, J., 1997. Vulnerability to cavitation in populations of two desert species, Hymenoclea salsola and Ambrosia dumosa, from different climatic regions. J. Exp. Bot. 48, 1323–1334.

Mencuccini, M., Grace, J., 1995. Climate influences the leaf area/sapwood area ratio in Scots pine. Tree Physiol. 15, 1–10.

Mencuccini, M., Grace, J., Fioravanti, M., 1997. Biomechanical and hydraulic determinants of tree structure in Scots pine: anatomical characteristics. Tree Physiol. 17, 105–113.

Mencuccini, M., Magnani, F., 2000. Comment on 'Hydraulic limitation of tree height: a critique' by Becker, Meinzer and Wullschleger. Funct. Ecol. 14, 135–137.

Milburn, J.A., 1991. Cavitation and embolisms in xylem conduits. In: Raghavendra, A.S. (Ed.), Physiology of Trees. Wiley, New York, pp. 163–174.

Milburn, J.A., 1996. Sap ascent in vascular plants: Challengers to the cohesion theory ignore the significance of immature xylem and the recycling of Münch water. Ann. Bot. 78, 399–407.

Milburn, J.A., Johnson, R.P.C., 1966. The conduction of sap. II. Detection of vibrations produced by sap cavitation in Ricinus xylem. Planta 69, 43–52.

Millikin Ishikawa, C., Bledsoe, C., 2000. Seasonal and diurnal patterns of soil water potential in the rhizosphere of blue oaks: evidence for hydraulic lift. Oecologia (in press).

Moreira, M.A., Sternberg, L.S.L., Nepstad, D.C., 2000. Vertical patterns of soil water uptake by plants in a primary forest and an abandoned pasture in the eastern Amazon: an isotopic approach. Plant Soil 222, 95–107.

Nardini, A., Pitt, F., 1999. Drought resistance of *Quercus pubescens* as a function of root hydraulic conductance, xylem embolism and hydraulic architecture. New Phytol. 143, 485–493.

Nardini, A., Tyree, M.T., 1999. Root and shoot hydraulic conductance of seven Quercus species. Ann. For. Sci. 56, 371–377.

Nardini, A., Logullo, M.A., Salleo, S., 1998. Seasonal changes of root hydraulic conductance (KRL) in four forest trees: an ecological interpretation. Plant Ecol. 139, 81–90.

Nardini, A., Logullo, M.A., Salleo, S., 1999. Competitive strategies for water availability in two Mediterranean Quercus species. Plant Cell Environ. 22, 109–116.

Nilsen, E.T., Sharifi, M.R., Rundel, P.W., Forseth, I.N., Ehleringer, J.R., 1990. Water relations of stem succulent trees in north-central Baja California. Oecologia 82, 299–303.

Nordhausen, M., 1919. Die Saugkraftleistungen abgeschnittener, transpirierender Sprosse. Ber. Deutsch Bot. Ges. 37, 443–449.

Passioura, J.B., 1982. Water in the soil–plant–atmosphere continuum. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), Physiological Plant Ecology II. Water Relations and Carbon Assimilation. Encyclopedia of Plant Physiology, New Series, vol. 12B. Springer-Verlag, Berlin, pp. 5–33.

Pataki, D.E., Oren, R., Phillips, N., 1998. Responses of sap flux and stomatal conductance of *Pinus taeda* L. Trees to stepwise reductions in leaf area. J. Exp. Bot. 49, 871–878.

Pate, J.S., Canny, M.J., 1999. Quantification of vessel embolisms by direct observation: a comparison of two methods. New Phytol. 141, 33–43.

Phillips, N., Nagchaudhuri, A., Oren, R., Katul, G., 1997. Time constant for water transport in loblolly pine trees estimated from time series of evaporative demand and stem sapflow. Trees — Struct. Function 11, 412–419.

Plumb, R.C., Bridgman, W.B., 1972. Ascent of sap in trees. Science 179, 1129–1131.

Pockman, W.T., Sperry, J.S., O'leary, J.W., 1995. Sustained and significant negative water-pressure in xylem. Nature 378, 715–716.

Renner, O., 1912. Versuche zur Mechanik der Wasserversorgung. 1. Der Druck in den Leitungsbahnen von Freilandpflanzen. Ber. Deutsch Bot. Ges. 30, 576–580.

Renner, O., 1925. Zum Nachweis negativer Drucke im Gefässwasser bewurzelter Holzgewächse. Flora 119, 402–408.

Richards, J.H., Caldwell, M.M., 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. Oecologia 73, 486–489.

Ritchie, G.A., Hinckley, T.M., 1971. Evidence for error in pressure-bomb estimates of stem xylem potentials. Ecology 30, 534–536.

Ryan, M.G., Binkley, D., Fownes, J.H., 1997. Age-related decline in forest productivity: Pattern and process. Adv. Ecol. Res. 27, 213–262.

Ryan, M.G., Yoder, B.J., 1997. Hydraulic limits to tree height and growth. Bioscience 47, 235–242.

Sakuratani, T., Aoe, T., Higuchi, H., 1999. Reverse flow in roots of *Sesbania rostrata* measured using the constant power heat method. Plant Cell Environ. 22, 1153–1160.

Saliendra, N.Z., Meinzer, F.C., 1989. Relationship between root/soil hydraulic properteis and stomatal behavior in sugarcane. Aust. J. Plant Physiol. 16, 241–250.

Saliendra, N.Z., Sperry, J.S., Comstock, J.P., 1995. Influence of leaf water status on stomatal response to humidity, hydraulic conductance, and soil drought in *Betula occidentalis*. Planta 196, 357–366.

Salleo, S., Hinckley, T.M., Kikuta, S.B., Logullo, M.A., Weilgony, P., Yoon, T.M., Richter, H., 1992. A method for inducing xylem emboli in situ-experiments with a field-grown tree. Plant Cell Environ. 15, 491–497.

Salleo, S., Logullo, M.A., DePaoli, D., Zippo, M., 1996. Xylem recovery from cavitation-induced embolism in young plants of *Laurus nobilis*: A possible mechanism. New Phytol. 132, 47–56.

Salleo, S., Logullo, M.A., 1989. Xylem cavitation in nodes and internodes of *Vitis vinifera* L. plants subjected to water stress: limits of restoration of water conduction in cavitated xylem conduits. In: Kreeb, K.H., Richter, H., Hinckley, T.M. (Eds.), Structural and Functional Responses to Environmental Stresses: Water Shortage. SPB Academic Publishing, The Hague, pp. 33–42.

Salleo, S., Nardini, A., Pitt, F., Logullo, M.A., 2000. Xylem cavitation and hydraulic control of stomatal conductance in Laurel (*Laurus nobilis* L.). Plant Cell Environ. 23, 71–79.

Schaeffer, S.M., Williams, D.G., 1998. Transpiration of desert riparian forest canopies estimated from sap flux. American Meteorological Society Special Symposium on Hydrology Paper P-2.10 (http://www.tucson.ars.ag.gov./salsa/archive/publications/ams_preprints/schaeffer.html)

Schmidt-Nielsen, K., 1984. Scaling: Why is Animal Size so Important? Cambridge University Press, Cambridge.

Scholander, P.F., Love, W.E., Kanwisher, J.W., 1955. The rise of sap in tall grapevines. Plant Physiol. 30, 93–104.

Scholander, P.F., Ruud, B., Leivestad, H., 1957. The rise of sap in a tropical liana. Plant Physiol. 32, 1–6.

Scholander, P.F., Hammel, H.T., Hemmingsen, E.A., Garey, W., 1962. Salt balance in mangroves. Plant Physiol. 37, 722–729.

Scholander, P.F., Hammel, H.T., Bradstreet, E.D., Hemmingsen, E.A., 1965. Sap pressure in vascular plants. Science 148, 339–346.

Schulze, E.-D., Cermak, J., Matyssek, R., Penka, M., Zimmermann, R., Vasicek, F., Gries, W., Kucera, J., 1985. Canopy transpiration and water fluxes in the trunk of Larix and Picea trees — a comparison of xylem flow, porometer, and cuvette measurements. Oecologia 66, 475–483.

Schulze, E.-D., Caldwell, M.M., Canadell, J., Mooney, H.A., Jackson, R.B., Parson, D., Scholes, R., Sala, O.E., Trimborn, P., 1998. Downward flux of water through roots (i.e. inverse hydraulic lift) in dry Kalahari sands. Oecologia 115, 460–462.

Sellin, A., 1994. Sapwood-heartwood proportion related to tree diameter, age and growth rate in Picea abies. Can. J. For. Res. 24, 1022–1028.

Smith, D.M., Jackson, N.A., Roberts, J.M., Ong, C.K., 1999. Reverse flow of sap in tree roots and downward siphoning of water by Grevillea robusta. Funct. Ecol. 13, 256–264.

Sobrado, M.A., Grace, J., Jarvis, P.G., 1992. The limits of xylem embolism recovery in Pinus sylvestris L. J. Exp. Bot. 43, 831–836.

Sperry, J.S., 1995. Limitations on stem water transport and their consequences. In: Gartner, B.L. (Ed.), Plant Stems: Physiological and Functional Morphology. Academic Press, San Diego, pp. 105–124.

Sperry, J.S., Ikeda, T., 1997. Xylem cavitation in roots and stems of Douglas fir and white fir. Tree Physiol. 17, 275–280.

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 Physiol. 100, 605–613.

Sperry, J.S., Tyree, M.T., 1990. Water-stress-induced xylem embolism in three species of conifers. Plant Cell Environ. 13, 427–436.

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

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

Sperry, J.S., Tyree, M.T., Donnelly, J.R., 1988c. Vulnerability of xylem to embolism in a mangrove vs. an inland species of rhizophoraceae. Physiol. Plant. 74, 276–283.

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., Cruziat, P., Davis, S., Ewers, F.W., Tyree, M.T., 1996. New evidence for large negative pressures and their measurement by the pressure chamber method. Plant Cell Environ. 19, 427–436.

Sprugel, D.G., Hinckley, T.M., Schaap, W., 1991. The theory and practice of branch autonomy. Annu. Rev. Ecol. Syst. 22, 309–334.

Sternberg, L.S.L., Swart, P.K., 1987. Utilization of fresh water and ocean water by coastal plants of southern Florida. Ecology 68, 1898–1905.

Stiller, V., Sperry, J.S., 1999. Canny's compensating pressure theory fails a test. Am. J. Bot. 86, 1082–1086.

Stratton, L.C., Goldstein, G., Meinzer, F.C., 2000a. Temporal and spatial partitioning of water resources among eight woody species in a Hawaiian dry forest. Oecologia 124, 309–317.

Stratton, L., Goldstein, G., Meinzer, F.C., 2000b. Stem water storage capacity and efficiency of water transport: their functional significance in a Hawaiian dry forest. Plant Cell Environ. 23, 99–106.

Teskey, R.O., Sheriff, D.W., 1996. Water use by Pinus radiata trees in a plantation. Tree Physiol. 16, 273–279.

Tsuda, M., Tyree, M.T., 1997. Whole-plant hydraulic resistance and vulnerability segmentation in Acer saccharinum. Tree Physiol. 17, 351–357.

Turner, N.C., Long, M.J., 1980. Errors arising from rapid loss in the measurement of leaf water potential by the pressure chamber technique. Aust. J. Plant Physiol. 7, 527–537.

Tyerman, S.D., Bohnert, H.J., Maurel, C., Steudle, E., Smith, J.A.C., 1999. Plant aquaporins: their molecular biology, biophysics and significance for plant water relations. J. Exp. Bot. 50, 1055–1071.

Tyree, M.T., 1999. The forgotten component of plant water potential: A reply-tissue pressures are not additive in the way M.J. Canny suggests. Plant Biol. 1, 598–601.

Tyree, M.T., Alexander, J.D., 1993. Hydraulic conductivity of branch junctions in three temperate tree species. Trees 7, 156–159.

Tyree, M.T., Dixon, M.A., 1983. Cavitation events in Thuja occidentalis L.? Ultrasonic acoustic emissions from the sapwood can be measured. Plant Physiol. 72, 1094–1099.

Tyree, M.T., Dixon, M.A., 1986. Water-stress induced cavitation and embolism in some woody-plants. Physiol. Plant 66, 397–405.

Tyree, M.T., Ewers, F.W., 1991. The hydraulic architecture of trees and other woody-plants. New Phytol. 119, 345–360.

Tyree, M.T., Ewers, F.W., 1996. Hydraulic architecture of woody tropical plants. In: Mulkey, S.S., Chazdon, R.L., Smith, A.P. (Eds.), Tropical Forest Plant Ecophysiology. Chapman and Hall, New York, pp. 217–243.

Tyree, M.T., Jarvis, P.G., 1982. Water in tissues and cells. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), Encyclopedia of Plant Physiology 12B, Springer-Verlag, Berlin, pp. 35–77.

Tyree, M.T., Sperry, J.S., 1989. Characterization and propagation of acoustic-emission signals in woody-plants-towards an improved acoustic-emission counter. Plant Cell Environ. 12, 371–382.

Tyree, M.T., Yang, S.D., 1990. Water-storage capacity of Thuja, Tsuga and Acer stems measured by dehydration isotherms — the contribution of capillary water and cavitation. Planta 182, 420–426.

Tyree, M.T., Yang, S.D., 1992. Hydraulic conductivity recovery versus water-pressure in xylem of *Acer saccharum*. Plant Physiol. 100, 669–676.

Tyree, M.T., Velez, V., Dalling, J.W., 1998. Growth dynamics of root and shoot hydraulic conductance in seedlings of five neotropical tree species: scaling to show possible adaptation to differing light regimes. Oecologia 114, 293–298.

Tyree, M.T., Fiscus, E.L., Wullschleger, S.D., Dixon, M.A., 1986. Detection of xylem cavitation in corn under field conditions. Plant Physiol. 82, 597–599.

Tyree, M.T., Patiño, S., Bennink, J., Alexander, J., 1995. Dynamic measurements of root hydraulic conductance using a high-pressure flowmeter in the laboratory and field. J. Exp. Bot. 46, 83–94.

Tyree, M.T., Yang, S.D., Cruiziat, P., Sinclair, B., 1994. Novel methods of measuring hydraulic conductivity of tree root systems and interpretation using amaized — a maize-root dynamic — model for water and solute transport. Plant Physiol. 104, 189–199.

Tyree, M.T., Cochard, H., Cruiziat, P., Sinclair, B., Ameglio, T., 1993a. Drought-induced leaf shedding in walnut — evidence for vulnerability segmentation. Plant Cell Environ. 16, 879–882.

Tyree, M.T., Salleo, S., Nardini, A., Logullo, M.A., Mosca, R., 1999. Refilling of embolized vessels in young stems of laurel. Do we need a new paradigm? Plant Physiol. 120, 11–21.

Tyree, M.T., Sinclair, B., Lu, P., Granier, A., 1993b. Whole shoot hydraulic resistance in Quercus species measured with a new high-pressure flowmeter. Ann. Sci. For. 50, 417–423.

Tyree, M.T., Snyderman, D.A., Wilmot, T.R., Machado, J.L., 1991. Water relations and hydraulic architecture of a tropical tree (*Schefflera morototoni*): data, models and a comparison with two temperate species (*Acer saccharum* and *Thuja occidentalis*). Plant Physiol. 96, 1105–1113.

Ursprung, A., Blum, G., 1916. Zur kenntnis der saugkraft. Ber. Deutsch Bot Ges. 34, 539–555.

Valentini, R., Scarabascia Mugnozza, G.E., Ehleringer, J.R., 1992. Hydrogen and carbon isotope ratios of selected species of a Mediterranean macchia ecosystem. Funct. Ecol. 6, 627–631.

Vertessy, R.A., Benyon, R.G., O'Sullivan, S.K., Gribbern, P.R., 1995. Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest. Tree Physiol. 15, 559–567.

Waring, R.H., Running, S.W., 1978. Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas fir. Plant Cell Environ. 1, 131–140.

Waring, R.H., Whitehead, D., Jarvis, P.G., 1979. The contribution of stored water to transpiration in Scots pine. Plant Cell Environ. 2, 309–318.

Wei, C., Tyree, M.T., Steudle, E., 1999. Direct measurement of xylem pressure in leaves of intact maize plants. A test of the cohesion-tension theory taking hydraulic architecture into consideration. Plant Physiol. 121, 1191–1205.

West, G.B., Brown, J.H., Enquist, B.J., 1999. A general model for the structure and allometry of plant vascular systems. Nature 400, 664–667.

White, J.W.C., Cook, E.R., Lawrence, J.R., Broecker, W.S., 1985. The D/H ratios of sap in trees: implications for water sources and tree ring D/H ratios. Geochim. Cosmochim. Acta 49, 237–246.

Whitehead, D., 1998. Regulation of stomatal conductance and transpiration in forest canopies. Tree Physiol. 18, 633–644.

Whitehead, D., Livingston, N.J., Kelliher, F.M., Hogan, K.P., Pepin, S., McSeveny, T.M., Byers, J.N., 1996. Response of transpiration and photosynthesis to a transient change in illuminated foliage area for a *Pinus radiata* D Don tree. Plant Cell Environ. 19, 949–957.

Wright, S.J., 1996. Phenological responses to seasonality in tropical forest plants. In: Mulkey, S.S., Chazdon, R.L., Smith, A.P. (Eds.), Tropical Forest Plant Ecophysiology. Chapman and Hall, New York, pp. 440–460.

Wullschleger, S.D., Meinzer, F.C., Vertessy, R.A., 1998. A review of whole-plant water use studies in trees. Tree Physiol. 18, 499–512.

Yang, S., Tyree, M.T., 1992. A theoretical-model of hydraulic conductivity recovery from embolism with comparison to experimental-data on *Acer saccharum*. Plant Cell Environ. 15, 633–643.

Yang, S.D., Tyree, M.T., 1993. Hydraulic resistance in *Acer saccharum* shoots and its influence on leaf water potential and transpiration. Tree Physiol. 12, 231–242.

Yang, S.D., Tyree, M.T., 1994. Hydraulic architecture of *Acer saccharum* and *A. rubrum* — comparison of branches to whole trees and the contribution of leaves to hydraulic resistance. J. Exp. Bot. 45, 179–186.

Yurtsever, Y., Gat, J.R., 1981. Atmospheric waters. In: Gat J.R., Gonfiantini R. (Eds.), Technical Report Series N. 210, Stable Isotope Hydrology. Deuterium and Oxygen-18 in the Water Cycle, International Atomic Energy Agency, Vienna, pp. 103–142

Zimmermann, G., Zhu, J.J., Benkert, R., Schneider, H., Thürmer, F., Zimmermann, U., 1995. Xylem pressure measurements in intact laboratory plants and excised organs: a critical evaluation of literature methods and the xylem pressure probe. In: Terazawa, M., McLeod, Ch. A., Tamal, Y. (Eds.), Tree Sap. Hokkaido University Press, Sapporo, pp. 47–58.

Zimmermann, M.H., 1978. Hydraulic architecture of some diffuse-porous trees. Can. J. Bot. 56, 2286–2295.

Zimmermann, M.H., 1983. Xylem structure and the ascent of sap. Springer-Verlag, New York

Zimmermann, U., Haase, A., Langbein, D., Meinzer, F.C., 1993. Mechanisms of long-distance water transport in plants: a re-examination of some paradigms in the light of new evidence. Phil. Trans. R. Soc. Lond. Ser. B 341, 19–31.

Zimmermann, U., Meinzer, F.C., Benkert, R., Zhu, J.J., Schneider, H., Goldstein, G., Kuchenbrod, E., Haase, A., 1994. Xylem water transport: Is the available evidence consistent with the cohesion theory? Plant Cell Environ. 17, 1169–1181.

Zotz, G., Tyree, M.T., Patiño, S., Carlton, M.R., 1998. Hydraulic architecture and water use of selected species from a lower montane forest in Panama. Trees 12, 302–309.

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

Zwieniecki, M.A., Hutyra, L., Thompson, M.V., Holbrook, N.M., 2000. Dynamic changes in petiole specific conductivity in red maple (*Acer rubrum* L.), tulip tree (*Liriodendron tulipifera* L.) and northern fox grape (*Vitis labrusca* L.). Plant Cell Environ. 23, 407–414.