Chapter 7

Forest Canopy Hydraulics

David R. Woodruff* and Frederick C. Meinzer
USDA Forest Service, Forestry Sciences Laboratory, Corvallis, OR 97331, USA

and

Katherine A. McCulloh
Department of Botany, University of Wisconsin-Madison, Madison, WI 53705, USA

*Author for correspondence, e-mail: dwoodruff@fs.fed.us

e-mail: rick.meinzer@oregonstate.edu

e-mail: kmcculloh@wisc.edu

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Summary

Water and carbon cycles are strongly coordinated and water availability is a primary limiting factor in many terrestrial ecosystems. Photosynthesis requires sufficient water supply to leaves and constraints on delivery at any point in the hydraulic continuum can lead to stomatal closure and reduced photosynthesis. Thus, maximizing water transport enhances assimilation and can provide plants with a competitive advantage. Unregulated water transport, however, can lead to excessive gradients in xylem tension that result in the development of air or vapor bubbles (i.e. embolisms) that block xylem water transport, potentially leading to permanent loss of function of the xylem. As such there can be a tradeoff between maximizing water transport and minimizing the risk of xylem embolism. This tradeoff has led to the development of a variety of hydraulic mechanisms to maximize efficiency and reduce vulnerability. Although several of these were first described centuries ago (such as stomatal control of transpiration), research in this field continues to uncover previously unrecognized processes employed by plants for maintaining hydraulic safety and/or efficiency. The hydraulic traits described in this chapter include xylem structural characteristics that enhance resistance to embolism such as pit and cell wall architecture; a continuum of strategies for constraining xylem tension to avoid embolism including isohydric and anisohydric control of leaf water potential; and safety and recovery mechanisms such as the capacitive discharge of stored water, hydraulic "circuit breakers" and the ability to repair xylem embolisms. Each of these will be discussed in terms of the variation in their use by contrasting tree types, their variability across organs and species, and their plasticity across environmental gradients. Beyond providing information about the means by which trees currently compete and survive, understanding the hydraulic mechanisms described in this chapter may provide insight into ways that trees are affected by, and the degree to which they may acclimate to rapidly changing climatic conditions.

I. Introduction

Ecosystem productivity is largely determined by the capacity for photosynthetic carbon assimilation and it is therefore heavily influenced by the hydraulic characteristics of the plants within the ecosystem. Hydraulic architecture, which we define as: "the structural and physiological characteristics that regulate the movement of water within a plant" is a means to explain plant water relations in the context of the cohesion tension theory of water movement in plants and the electrical analogy used to characterize water transport within the soil-plant water continuum using flow, water potential (Ψ), capacitance and resistance. Martin Zimmermann coined the term "hydraulic architecture" in the 1970s to describe patterns of hydraulic resistances in plants (Zimmermann 1978). Since then,

Symbols and Definitions: A_l:A_s – Leaf area to sapwood area ratio; d_a – Pit aperture depth; D_a – Pit aperture diameter; D_l – Conduit lumen diameter; g_s – Stomatal conductance; HR – Hydraulic redistribution; k – Hydraulic conductivity; k_l – Leaf specific hydraulic conductivity; k_s – Sapwood specific hydraulic conductivity; K_h – Hydraulic conductance; K_{leaf} – Leaf hydraulic conductance; K_{plant} – Whole plant hydraulic conductance; L – Conduit length; l_a – Pit aperture length; n_{pi} – Total number of pits per conduit; P_{50} – 50 % loss of hydraulic conductivity/conductance; P_e – Threshold pressure for conduit air entry; R_b – Radius of a bubble; R_h – Hydraulic resistance; R_{lum} – Conduit lumen resistance; R_{pit} – Conduit end wall pit resistance; $R_{pit\text{-}total}$ – Total conduit pit resistance; R_{tot} – Total conduit resistance; T – Surface tension of water; ρ – Density of water; υ – Viscosity of water; Ψ – Water potential; Ψ_{leaf} – Leaf water potential; Ψ_{soil} – Soil water potential

hydraulic architecture has come to include a broad range of mechanisms that plants have developed to maintain efficient and safe water transport and new discoveries are being made continuously. In order to understand the significance of these mechanisms it is helpful to recognize that the different components of a plant's hydraulic system face distinct challenges, just as they each play different roles in water transport. Although many of the principles in this chapter are applicable to all plants; hydraulics in woody plants, and in particular trees, involves additional challenges and adaptations that influence the transport of water from roots to leaves. It is for this reason that our focus in this chapter is on trees. To a great extent, the components of hydraulic architecture described in this chapter that are associated with leaves are likely applicable to herbaceous canopies (Meinzer and Grantz 1990; Mencuccini 2003).

A. Components of the Hydraulic Transport System

Water moves through trees via a continuous water column from the soil to the site of evaporation within the leaves. The transport of water through xylem generally occurs under tension (or negative pressure) and along a gradient of increasing tension, i.e. along a gradient of water potential (Ψ) from less to more negative. The ability of water to be transported through xylem is described in terms of hydraulic conductance (K_h). K_h is the change in flow rate of liquid water through a system per change in hydraulic pressure driving the flow, and the inverse of K_h is hydraulic resistance (R_h). Leaves, stems and roots comprise different components of a plant's hydraulic system and stomata are intimately linked to the function of each of these through their control of transpiration. Each of these is influenced by different constraints on water transport and each is characterized by different attributes that mitigate these constraints. Stomata maintain the integrity of the soil-to-leaf hydraulic continuum by regulating transpiration of water vapor, and stomatal resistance to transpiration is typically at least two orders of magnitude greater than the hydraulic resistance to bulk water flow of the entire plant (Sack and Tyree 2005). Although transpiration rate is largely determined by stomatal conductance (g_s), leaf water potential (Ψ_{leaf}) has a direct impact on g_s and Ψ_{leaf} at a given transpiration rate is strongly influenced by whole plant hydraulic conductance (K_{plant}; Tyree and Zimmermann 2002). As such, transpiration is strongly influenced by a number of aspects of hydraulic architecture along the hydraulic continuum from roots to leaves.

The response of stomata to changes in plant water status has been described as that of a "pressure regulator" (Sperry et al. 2002). Just as a pressure regulator limits pressure by controlling flow rate, stomata limit the degree of xylem tension due to soil moisture depletion and evaporative demand by reducing transpiration. Stomata will reduce transpiration, and thus photosynthesis, when declining leaf water status decreases the turgor in the guard cells (relative to epidermal cells) leading to stomatal closure and a reduction in g_s. The immediate link between changes in g_s and the ability of plants to acquire carbon makes stomatal function a critically important factor in the water and carbon cycles of terrestrial ecosystems (Farquhar and Sharkey 1982). The precise mechanisms of stomatal control of plant water balance can be difficult to resolve because at any given moment stomata may be responding to an intricate array of environmental factors including light level, light quality, vapor pressure deficit and CO_2 concentration. Although root mediated signals of hormones such as ABA and cytokinin strongly influence stomatal conductance by changing the permeability of guard cell membranes (Wilkinson and Davies 2002), the rapid response of stomata to reduced root area (Meinzer and Grantz 1990), increased root xylem embolism (Alder et al. 1996), decreased shoot conductivity (Salleo et al. 2000) and increased xylem embolism within leaves (Nardini et al. 2001) illustrates that stomatal conductance responds to signals within the plant that are related to changes in hydraulic architecture, and which are able to travel more rapidly than root mediated hormone signals.

Leaf hydraulic conductance (K_{leaf}) is a measure of the rate of water flow through the xylem and extraxylary pathways to the sites of evaporation within the leaf, divided by the water potential difference across the leaf ($\Delta\Psi_{leaf}$), which is the driving force for flow. Leaves comprise an estimated 25 % (Sack et al. 2003) to 80 % (Nardini et al. 2001) of the total hydraulic resistance within plants. Although leaves exist at the terminal end of the hydraulic transport system and are therefore prone to experience higher xylem tensions than other plant organs, they are generally, although not always, more vulnerable to embolism than stems (Johnson et al. 2011). As such, leaves invariably represent a potential hydraulic bottleneck. K_{leaf} is strongly correlated with both maximum photosynthesis and stomatal conductance in temperate deciduous trees (Aasamaa et al. 2001), which highlights the importance of K_{leaf} in influencing gas exchange and therefore productivity of individual plants and ecosystems. Research examining the connections between leaf structural characteristics and transport efficiency has begun to identify the ways in which trade-offs between efficiency and safety manifest themselves in leaf anatomical characteristics (Aasamaa et al. 2005; Sack and Frole 2006; Woodruff et al. 2008).

In addition to transporting water from roots to leaves, stems also provide mechanical support to resist the forces of wind, snow loading and gravity. One way that the xylem conduits of conifers (tracheids) differ from those of angiosperms (generally vessels) is that tracheids are the sole source of mechanical support for the stem, whereas vessels are surrounded by sclerenchyma tissues that contribute mechanical support. In tracheids the increased wall thickness to span ratio that is needed to provide stems with sufficient mechanical strength represents an increased construction cost that is consistent with a trade-off between safety and efficiency (Pittermann et al. 2006). Roots play less of a role in providing mechanical support relative to stems, however roots tend to be very efficient at transporting water. Root xylem conduits tend to have larger lumen diameters and higher conductivity per sapwood cross-sectional area (specific conductivity, k_s) than other tissues (McElrone et al. 2004). They are also more prone to reaching minimum xylem pressures that are closer to levels that are associated with relatively high losses of conductance (i.e. they tend to operate under narrower safety margins than stems; Sperry and Saliendra 1994; Alder et al. 1996; Martínez-Vilalta et al. 2002). Although the narrow safety margins under which roots operate make them potentially more vulnerable to high levels of embolism, it has been argued that root conduits are easier to refill due to the relatively high water potentials of surrounding soil (Sperry and Saliendra 1994), and that they are easier to replace and "less expensive" in terms of carbon investment than stems (Kolb and Sperry 1999; Hacke et al. 2000).

B. Constraints on Hydraulic Transport

The overall water transport pathway from the root-soil interface to the atmosphere can be characterized as consisting of a series of resistances (Fig. 7.1). Each plant organ along this hydraulic continuum is composed of water conducting structures that vary functionally and anatomically across species, ontogeny and location (i.e. root, stem, leaf) within an individual plant. The water conducting portion of a tree's vascular system is composed of tracheids for conifers and vessels in angiosperms (except for some vessel-less species), collectively referred to as conduits. Hydraulic conductance is strongly influenced by the structural characteristics of xylem conduits such as lumen diameter, conduit length and pit characteristics such as pit aperture size and pit membrane pore characteristics. According to the Hagen-Poiseuille equation, even minor changes in conduit lumen diameter (D_l) lead to substantial changes in transport efficiency:

$$R_{lum} = 128\ \upsilon L/\pi\rho D_l^4, \qquad (7.1)$$

where R_{lum} is resistance associated with conduit lumens, υ is the viscosity of water (1.002×10^{-9} MPa s at 20 °C), L is conduit length, and ρ is the density of water

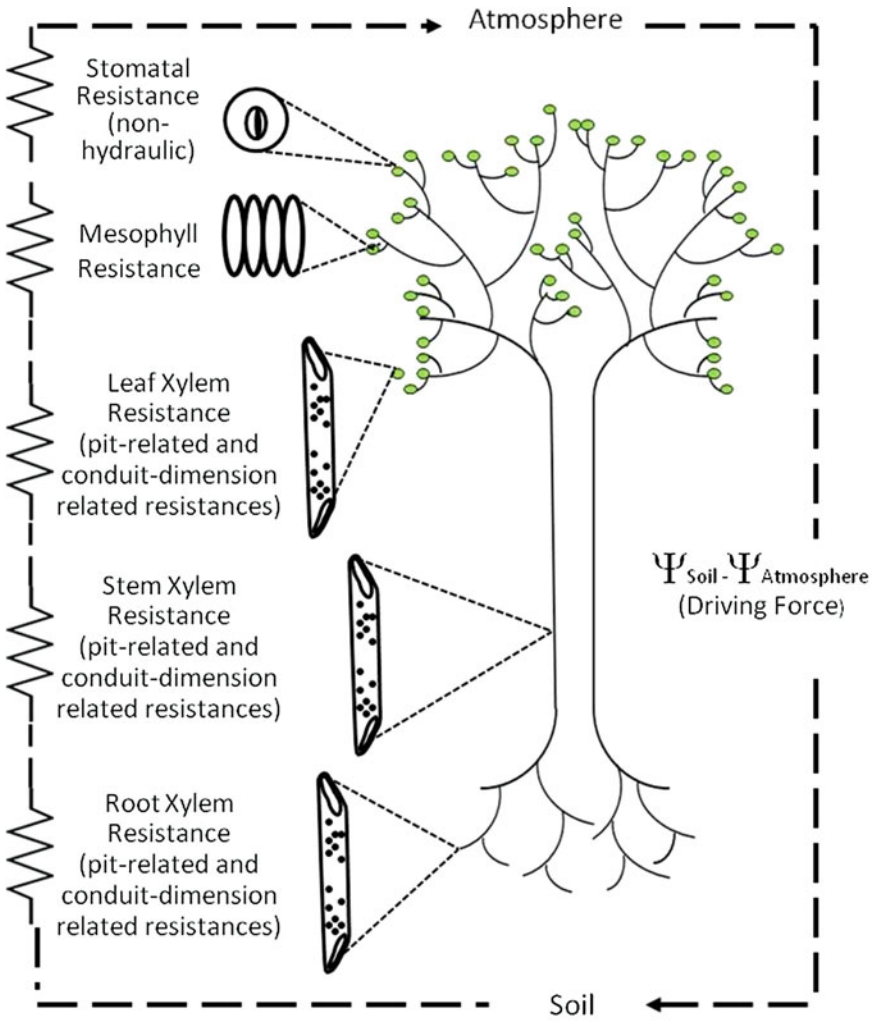

Fig. 7.1. A schematic of hydraulic resistances in series within a tree from soil to the stomata and the driving force for transport

(5.55×10^7 mmol m^{-3}). Because of the fourth power relationship between lumen diameter and hydraulic resistance, a doubling of lumen diameter for example results in a 16-fold increase in hydraulic conductance.

Xylem hydraulic conductance is also substantially impacted by the pitted walls that separate adjacent conduits. Although evaluating hydraulic characteristics at the pit level is inherently difficult due to the small size of pits, a great deal of progress has been made in evaluating the role of pits in maintaining hydraulic safety and constraining hydraulic efficiency. Pit resistivity is largely determined by pit aperture resistance (R_{pit}) (Hacke et al. 2004; Domec et al. 2006a), and the resistance of a conduit's pit aperture can be modeled as a circular opening, the length of which is equivalent to the depth of the pit aperture. Dagan et al. (1982) adapted the following relationship from the Hagen Poiseuille equation to provide an approximate solution for the hydraulic resistance of circular pit pores of finite length:

$$R_{pit} = 24\upsilon/\left(D_a^3\right) + 128 l_a \ \upsilon/\left(\pi D_a^4\right), \qquad (7.2)$$

where D_a is pit aperture diameter and l_a is pit aperture length, taken as half the difference between the thickness of the whole pit and the thickness of the pit chamber. Resistances

are additive in a series by Ohm's law analogy so a conduit's total resistance (R_{tot}) is determined by both R_{lum} and the total contribution of conduit pits to conduit resistance ($R_{pit\text{-}total}$):

$$R_{tot} = R_{lum} + R_{pit\text{-}total}, \quad (7.3)$$

with $R_{pit\text{-}total}$ being determined by both R_{pit} and the total number of pits per conduit (n_{pi}):

$$R_{pit\text{-}total} = R_{pit}/n_{pi}. \quad (7.4)$$

The hydraulic resistance associated with pits has been estimated to represent between 14 and 84 % of the total hydraulic resistance across a number of species (Schulte and Gibson 1988), and other studies have provided estimates of approximately 50 % for the proportion of hydraulic resistance associated with conduit end walls across a range of xylem structures in both tracheid and vessel-bearing species (Sperry et al. 2005; Choat et al. 2008). Conduit length can also have a significant impact on transport efficiency because a decrease in conduit length increases the total number of conduit end-walls that are traversed for a given distance of water transport in the xylem. As such, any increase in mean conduit length results in a decrease in cumulative end-wall resistance for a given pit structure.

C. Hydraulic Vulnerability

As stated earlier, the transport of water through xylem generally occurs under tension (or negative pressure) and along a gradient of increasing tension. The tension results from both frictional resistance during water transport as well as gravitational forces that lead to a 0.01 MPa increase in tension per meter increase in height. If this tension exceeds a critical level, air can be pulled in from adjacent tissues resulting in embolism. Surface tension and the structure and function of the membranes in the pitted end-walls that connect conduits typically block embolisms from moving to adjacent conduits, but not always. Embolisms can substantially decrease the hydraulic conductivity of a plant organ thereby limiting the ability for trees to transpire and assimilate carbon. Figure 7.2 illustrates the relationships between xylem tension, conduit embolism and water transport (in this case in leaves). Figure 7.2a–c are cryo-scanning electron microscope images of Douglas-fir leaf tracheids that show tracheids that are full of water at the time of freezing ($\Psi_{leaf} = -0.5$ MPa), tracheids that are devoid of water ($\Psi_{leaf} = -2.1$ MPa) and what appears to be a transitional phase where tracheids are partially filled with water ($\Psi_{leaf} = -1.5$ MPa), respectively. Panel D represents a hydraulic vulnerability curve of foliage from the same branch as the images in Fig. 7.2a–c in which the y-axis represents K_{leaf} and the x-axis represents Ψ_{leaf}. As the xylem tension increases (represented by increasingly negative Ψ_{leaf}) K_{leaf} declines. The levels of Ψ_{leaf} represented by the images in Fig 7.2a–2c are indicated by arrows in the vulnerability curve. The ability of xylem to avoid or resist cavitation and embolism is a measure of hydraulic safety and it is broadly recognized that enhanced safety often comes at the price of reduced efficiency (Zimmermann 1983; Tyree et al. 1994; Sperry et al. 2008).

II. Safety and Efficiency of Hydraulic Architecture

The metastable state under which water is transported in the xylem means that there is a risk of an air bubble, or embolism, disrupting the flow. If constructing a xylem that is safer from these embolisms means that the hydraulic conductance of the network is reduced, there is a tradeoff between hydraulic safety and efficiency. The focus of this section is on causes and consequences of embolism propagation, recovery from embolisms, and the integration of stomatal control and hydraulic function.

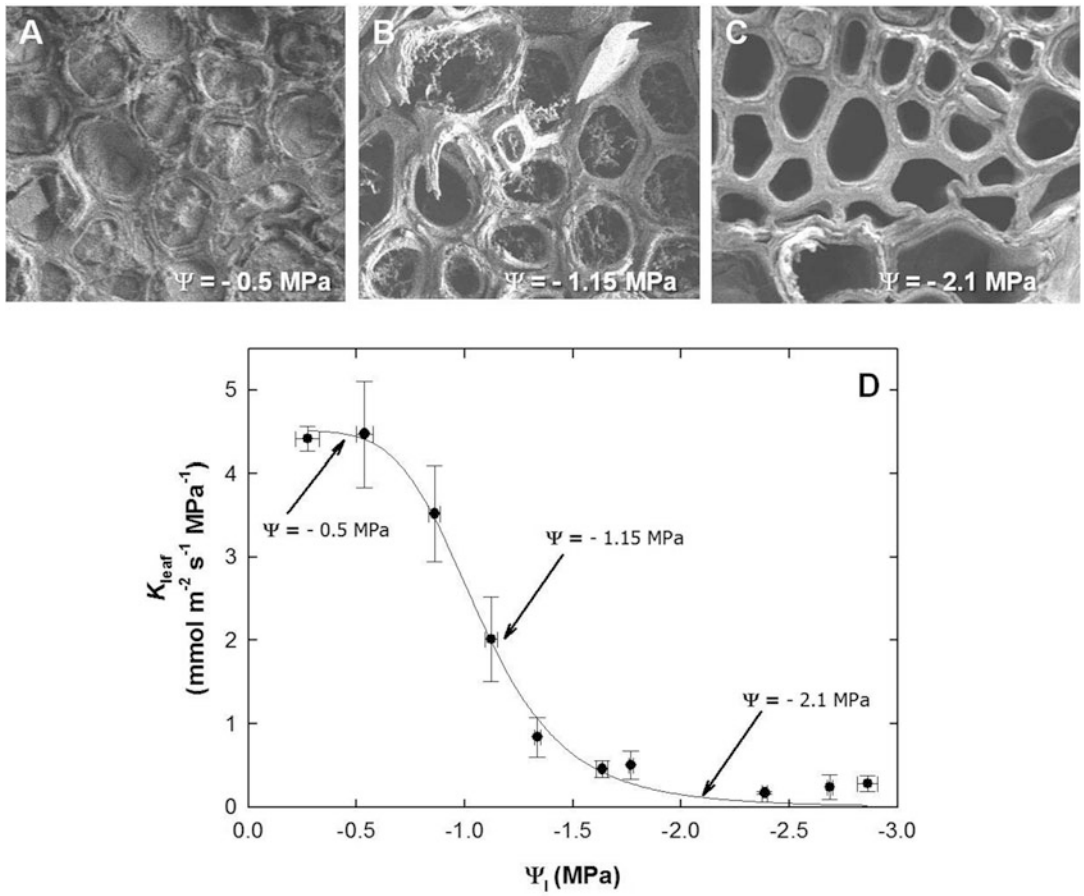

Fig. 7.2. Cryo-scanning electron microscopy (Cryo-SEM) images of Douglas-fir leaf tracheids frozen at a range of leaf water potentials (**a, b, c**) and the relationship between leaf hydraulic conductance and leaf water potential (**d**). Leaf water potential = −0.05 MPa with leaf tracheids predominantly full (**a**). Leaf water potential = −1.15 MPa with leaf tracheids partially full (**b**); and leaf water potential = −2.1 MPa with leaf tracheids predominantly empty (**c**). The three leaf water potentials represented in the Cryo-sem images are indicated by arrows in panel D. Adapted from Woodruff et al. (2007)

A. Embolism Formation and Avoidance

The functional consequence of embolism proliferation is a drop in the hydraulic conductance of the network, and this propagation occurs primarily in two ways. The first cause is due to air-seeding from one conduit to a neighboring conduit and is due to a decline in the xylem pressure because of drought stress. The sites of air-seeding between neighboring conduits are pit membranes (Crombie et al. 1985; Cochard et al. 1992), which are passageways for water to pass when both conduits are functional. These two-way valves are made of primary wall material, and are not "membranes" in the lipid-bilayer sense of the term. The pit membrane rests in the center of the pit chamber when both conduits are water-filled, but gets sucked over to cover the pit aperture by the negative pressure of the water in the functional conduit when the neighboring conduit becomes embolized (Siau et al. 1984). When water stress causes the pressure in the functional conduit to drop below the threshold value that pulls a bubble across the membrane (in angiosperms) or pulls part of the pit membrane into the aperture and

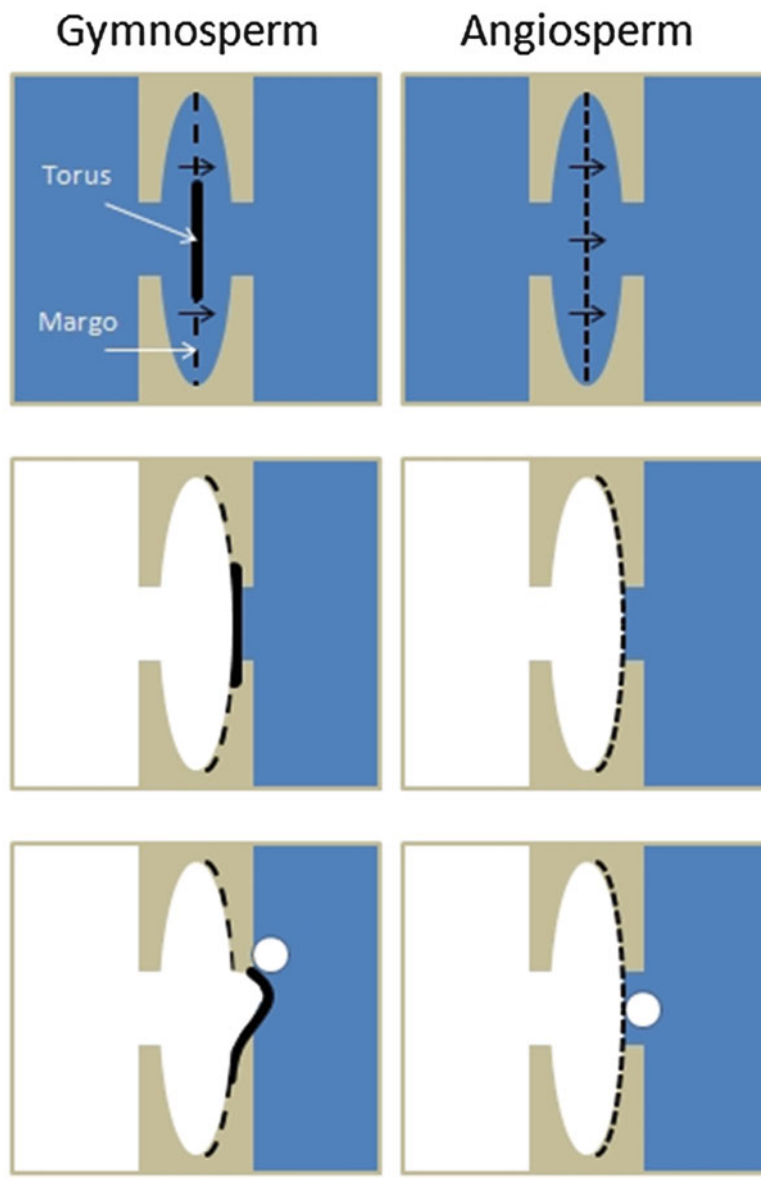

Fig. 7.3. Pit membranes connecting neighboring conduits in gymnosperms and angiosperms. The *top panels* show that water can flow through the pores throughout the homogeneous angiosperm pit and through the porous margo in the gymnosperm pit, but not through its thickened torus. The *middle panels* depict how the pits of each group seal the pit aperture when the conduit on the *left* becomes embolized and the conduit on the *right* remains functional. The *bottom panels* illustrate how a bubble can propagate from one embolized conduit to a functional one through a process called air-seeding. Adapted from Hacke et al. (2004) with permission

allows an air bubble to follow (in conifers), the functional conduit embolizes and becomes non-functional.

The distinction in how the air-seeding occurs in angiosperms vs. conifers is due to the differences in their pit membrane morphology (Fig. 7.3). In angiosperms, the membrane is a homogenous mesh-like network of primary cell wall material, and the air-seeding pressure is only limited by the tensile strength of water. Thus, one theory of what determines air-seeding in angiosperms is the "pit area" or "rare pit" hypothesis, which postulates that the vulnerability of a conduit to water-stress induced embolism increases with the proportion of the conduit wall that is covered by pits (Hargrave et al. 1994; Wheeler et al. 2005; Sperry et al. 2006; Choat et al. 2008; Christman et al. 2009, 2012). This correlation is not due to the collective area of pits, but instead because a greater pit area

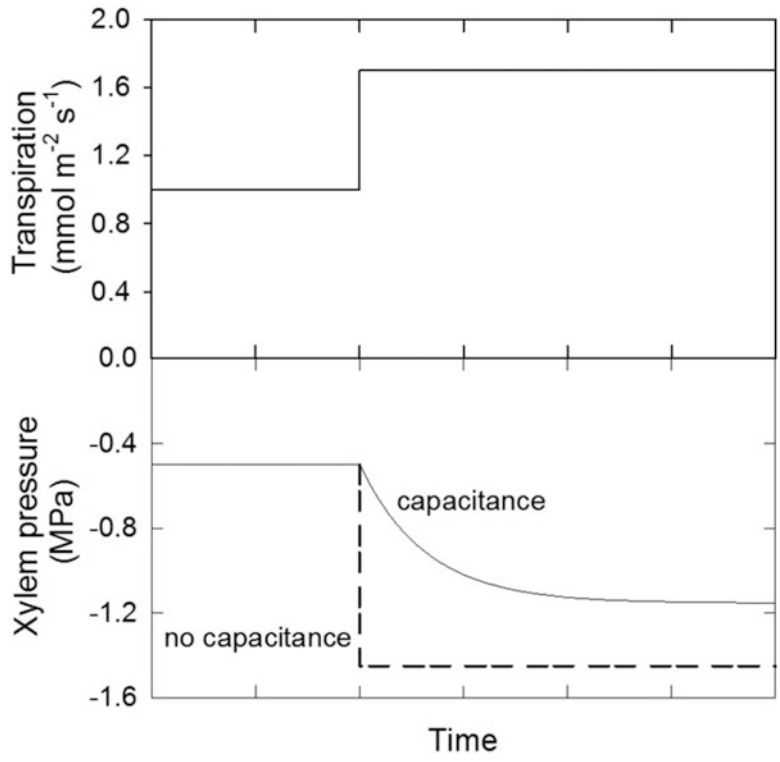

Fig. 7.4. A theoretical example showing the impact of an increase in transpiration (*top panel*) on the xylem pressure in a species with capacitance and a hypothetical one without capacitance (*bottom panel*)

increases the likelihood of having a rare pit pore that is larger than the others and therefore allows air to seed at a smaller pressure difference. A tradeoff exists between hydraulic safety and conducting efficiency because the smaller proportion of wall covered in pits in safer vessels reduces the hydraulic conductance of the network. Conifers, in contrast, have pits with two distinct regions (Bauch et al. 1972). The central region, which is very tightly knit primary cell wall material and does not allow water or air to pass through it, is called the torus. Surrounding the torus is the margo, which is made up of very loosely organized microfibrils. It is through this region that the water passes when both tracheids are functional. The division of labor between the sealing torus and the porous margo means that air-seeding is not the result of a rare, large pit pore as in angiosperms. Instead, the ratio of the torus diameter to the pit aperture diameter seems to determine the vulnerability of a pit to seeding air (Burgess et al. 2006; Domec et al. 2006a, 2008; Hacke and Jansen 2009; Delzon et al. 2010). In conduits that have a large overlap of torus to aperture, greater pressure difference is required between the tracheids to dislodge the pit membrane and allow air to be sucked into the functional tracheid. A tradeoff exists between hydraulic safety and conducting efficiency because the smaller pit aperture of a safer pit has a lower hydraulic conductance (Domec et al. 2008).

At the tissue scale, there are three main parameters that correlate with safety from embolism propagation due to drought stress. First, the ability of a tissue to store water, or its capacitance, buffers the speed of declines in xylem pressure with increases in transpiration (Fig. 7.4), which may provide stomata the time needed to limit transpiration, thus protecting the xylem from embolism-inducing negative pressures (Fig. 7.4). Species with greater capacitance tend to experience milder leaf water potentials at midday (Meinzer et al. 2003; Santiago et al. 2004;

Borchert and Pockman 2005; McCulloh et al. 2012), have lower wood density (Pratt et al. 2007; Meinzer et al. 2003, 2008a), and less negative xylem pressures that result in 50 % loss of hydraulic conductivity (P_{50}, see below) (Domec and Gartner 2001; Pratt et al. 2007; Meinzer et al. 2009). See Sect. III.C of this chapter for further discussion on capacitance.

The second parameter that correlates with drought safety is wood density. Stems with higher wood density tend to have more negative P_{50}s (Hacke et al. 2001; Pratt et al. 2007; Chave et al. 2009; Hoffmann et al. 2011; Markesteijn et al. 2011; Ogasa et al. 2013), yet wood density does not, inherently, provide any known protection against air seeding. The mechanistic link between hydraulic safety and wood density seems to be the result of the thicker walls needed to withstand the lower operating pressures that drought-tolerant species experience. Specifically, species with more negative P_{50}s have a wider double-wall thickness between neighboring conduits for a given mean hydraulic diameter, which is a hydraulic conductivity-weighted average lumen diameter (Hacke et al. 2001). Compared with angiosperms, conifers are able to tolerate a more negative P_{50} with a given wood density. Although robust support for this correlation exists across species, within a species the pattern is not always observed (Bucci et al. 2006; Domec et al. 2009).

The third tissue-level factor is the link between the degree of inter-connectedness of vessels and hydraulic safety, and this is the most causal of the three parameters. Given that air seeding occurs at the level of the pit, the safest vessels are ones that have no or very few pit connections. Indeed, where it has been examined, greater resistance to embolism has been observed in species with fewer vessels in contact with one another, and this drought resistance has come at the cost of reduced hydraulic conductivity (Zanne et al. 2006; Ewers et al. 2007a; Loepfe et al. 2007; Schenk et al. 2008; Lens et al. 2011; Martínez-Vilalta et al. 2012; Brodersen et al. 2012). Due to their short conduits and inherently interconnected xylem network, tracheid bearing species like conifers, cannot alter this parameter.

The second way that emboli form in conduits is because of freeze-thaw cycles (Sucoff 1969; Robson et al. 1988). The "thaw-expansion" hypothesis posits that air that had been dissolved in xylem water forms bubbles in conduits when that water freezes. When the ice thaws, that bubble can either redissolve or expand to fill the conduit and form an embolism. Which of these two options occurs depends on the pressure of the xylem water (Pittermann and Sperry 2006) as described by La Place's law (Yang and Tyree 1992). The bubble will expand or collapse if the xylem pressure is, respectively, less than or greater than $-2\ T/R_b$, where T is the surface tension of water (0.0728 Pa m) and R_b is the radius of the bubble, which in xylem conduits is roughly the diameter of the conduit (Tyree and Zimmermann 2002). The link between the conduit diameter, bubble diameter and the pressure required to dissolve bubbles means two things. First, it means that narrower conduits tend to be less susceptible to loss of hydraulic conductivity from single freeze-thaw events, and this pattern has been observed in both conifers (Sperry and Robson 2001; Pittermann and Sperry 2003, 2006) and angiosperms (Davis et al. 1999; Feild et al. 2002). Second, it means that more negative xylem pressure prior to freezing leads to more embolisms, and a number of studies have observed a large drop in hydraulic conductivity caused by freeze-thaw cycles coupled with drought (Lemoine et al. 1999; Sparks and Black 2000; Sparks et al. 2001; Mayr et al. 2002, 2003). Seemingly wet environments can create more drought-like stress than expected in cold months, because the hydraulic conductance of water through the soil is severely reduced as water becomes more viscous (Wan et al. 2001; Pregitzer and King 2005), and membrane transport properties are altered because of the impact of reduced aquaporin production (Yu et al. 2006; Murai-Hatano et al. 2008).

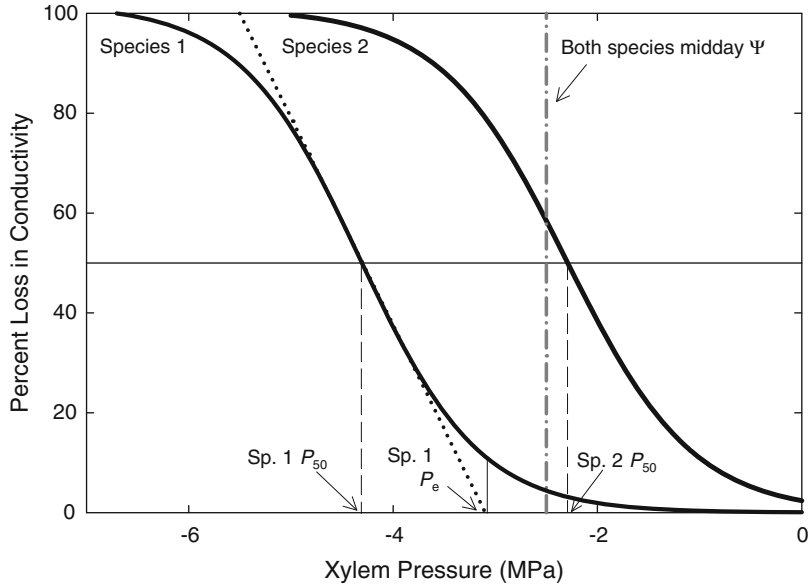

Fig. 7.5. Two theoretical vulnerability curves from organs (e.g., roots, stems or leaves) of two species. The horizontal line shows the point of 50 % loss of hydraulic conductivity, and the x-axis value where this line intersects with each vulnerability curve is the P_{50} (*dashed drop lines*). The *vertical dot-dash line* is the midday water potential value (Ψ), which for simplicity is the same for both species in this example. The difference between the midday water potential and the P_{50} for each species is an example of a hydraulic safety margin. The *vertical solid line* indicates the P_e for Species 1, which indicates an inflection point on the curve after which the percent loss in conductivity increases rapidly. The P_e for Species 2 is not shown for simplicity

Embolisms caused by freeze-thaw cycles may be avoided by having small diameter conduits, or they can be tolerated by one of two solutions. First, some species refill embolized conduits in the spring either through stem pressure, root pressure, or possibly by absorbing water through distal plant parts. Stem pressure has been well documented in species in which the sap is economically important, such as in maples, but the details of the mechanism are still a matter of dispute (Tyree and Zimmermann 2002). Other species, such as grapevine, create substantial root pressure in the spring to refill vessels (Sperry et al. 1987). Four species of conifer showed substantial recovery from freeze-thaw-induced loss of hydraulic conductivity that could not be explained by stem or root pressure, or growth of new wood (McCulloh et al. 2011a, b). The second solution is to simply grow new vessels. Ring-porous species, which grow 1–2 rings of very wide vessels in the spring and then fibers and much smaller vessels for the rest of the growing season, use this approach. Ring-porosity is a uniquely northern hemisphere solution to the problem of freeze-thaw induced emboli (Wheeler et al. 2007).

B. Functional Implications of the Loss and Recovery of Hydraulic Function

Although plants have many mechanisms to avoid embolism propagation, loss of hydraulic conductance or conductivity does occur. We measure the decline of hydraulic function with water stress by creating vulnerability curves (Fig. 7.5). There are various metrics used to compare these curves across species, but two commonly used ones are the P_{50} (see above) and P_e, which is the threshold pressure for air entry. The P_e is particularly important, because pressures even slightly more negative than it result in large increases in the percent loss of hydraulic conductivity. Although some species attempt

to avoid loss of hydraulic conductance during normal daily cycles of water stress by employing the structural features described above, others tend to lose conductance in one or more distal organs (i.e., leaves, twigs, or rootlets) every day and then regain function overnight (Zwieniecki and Holbrook 1998; Bucci et al. 2003; Trifilò et al. 2003; Brodribb and Holbrook 2004; Stiller et al. 2005; Johnson et al. 2009, 2011). The latter strategy effectively creates a circuit breaker that hydraulically isolates the downstream portions of the plant and causes stomatal closure (Johnson et al. 2012). This idea of a circuit breaker signaling stomatal closure was well characterized in Douglas-fir needle-bearing shoots in which a strong correlation was found between the water potentials at which shoot hydraulic conductance drops to its minimum value and at which stomata close (Woodruff et al. 2007).

One way to determine the threat of hydraulic failure is with hydraulic safety margins (Fig. 7.5; Meinzer et al. 2009; Johnson et al. 2012; Choat et al. 2012). These metrics represent the difference between the xylem tension (or negative pressure) at a specified loss of xylem hydraulic conductivity (e.g., the P_{50} of a root, stem or leaf) and the point where a physiological mechanism engages to limit transpiration and xylem tension (e.g., the midday water potential of that organ). Some species operate under wide margins of hydraulic safety (e.g., Species 1 in Fig. 7.5) and others under narrow margins (Pockman and Sperry 2000; Brodribb et al. 2003; Brodribb and Holbrook 2004; Pratt et al. 2007; Meinzer et al. 2009; Bucci et al. 2012; Johnson et al. 2012; Choat et al. 2012). Safety margins can also differ in organs such as leaves, stems and roots within a species, and the pattern among organs can vary considerably among species with some species exhibiting smaller margins in the leaves than stems and other species showing the opposite pattern (e.g., Hao et al. 2008; Chen et al. 2009). However, it is crucial to bear in mind that some species are able to refill embolized conduits on daily or seasonal bases, and, thus, these safety margins may not accurately reflect the inherent risk that loss of hydraulic conductivity was previously thought to cause.

As described above, embolisms can be refilled when the pressure in the xylem is less negative than the pressure required to dissolve a bubble in a conduit as described by La Place's law (Yang and Tyree 1992). Relatively recently it has also become clear that bubbles can be dissolved when the surrounding xylem pressure is below what La Place's law would predict to be necessary. This "novel refilling" (Hacke and Sperry 2003) was first described after *Laurus nobilis* was shown to regain hydraulic conductivity after emboli were induced by injecting air into stems of intact plants (Salleo et al. 1996; Tyree et al. 1999) and in situ in three species of different wood type that experienced normal daily cycles of water stress (Zwieniecki and Holbrook 1998). Since then, it has been observed extensively in leaves (Bucci et al. 2003; Trifilò et al. 2003; Brodribb and Holbrook 2004; Stiller et al. 2005; Nardini et al. 2008; Johnson et al. 2009, 2011), roots (McCully et al. 1998; McCully 1999; Domec et al. 2006b), and stems (Brodersen et al. 2010; Hacke and Sperry 2003; Taneda and Sperry 2008; Christman et al. 2012). While the mechanism of this refilling remains uncharacterized, it is thought that sugars are imported into embolized conduits, which creates an osmotic gradient that draws water into the conduit from the surrounding tissue (Zwieniecki and Holbrook 2009; Nardini et al. 2011a).

The extent to which plants can recover from embolisms differs between species as well as between different plant parts. When the hydraulic safety margins of angiosperm and conifer small diameter stems are compared, angiosperms tend to have narrower or even negative margins (indicating that the midday water potential should result in significant losses of conductivity; e.g., Species 2 in Fig. 7.5) compared with the wider margins of conifers (Meinzer et al. 2009; Johnson et al. 2012; Choat et al. 2012). Thus, stems of many angiosperm species seem to undergo daily cycles of hydraulic

conductance loss and recovery (Zwieniecki and Holbrook 1998; Taneda and Sperry 2008; Brodersen et al. 2010; Christman et al. 2012; Ogasa et al. 2013), while conifer stems may only lose small amounts or no hydraulic conductivity daily (Zwieniecki and Holbrook 1998). One proposed explanation for this difference is the smaller fraction of living cells in conifer than angiosperm wood, which may limit the ability of conifer stems to quickly or efficiently deliver the sugars necessary to refill under negative pressure (Johnson et al. 2012). It is worth noting that the distinction of whether a species commonly undergoes cycles of conductivity loss and recovery in stems or not is not clearly delineated by taxa (i.e., conifers vs. angiosperms). Instead, there appears to be a continuum of the fraction of wood devoted to living cells, and this correlates negatively with hydraulic safety margin. However, in contrast to the often wide safety margins in their stems, the needles of many conifer species undergo daily cycles of hydraulic conductance loss and recovery (Woodruff et al. 2007; Johnson et al. 2009, 2011). Given the ability of plants to recover from embolisms, it is becoming increasingly clear that static variables such as P_{50} are not adequate to characterize a plant's response to water stress. Indeed, Ogasa et al. (2013) found that species with less negative P_{50}s had a greater ability to recover from embolism than those with more negative P_{50}s.

Although considerable research is currently focused on novel refilling, many questions remain. An obvious area of research focus is on the actual mechanism of novel refilling (Salleo et al. 2004, 2006, 2009; Zwieniecki and Holbrook 2009; Nardini et al. 2011a). Another open question is whether there are trends with respect to the location of hydraulic circuit breakers that correlate with wood type or with plant phylogeny. The Pinaceae that have been examined, for instance, all lose nearly all or their entire leaf hydraulic conductance on a daily basis (Woodruff et al. 2007; Johnson et al. 2009, 2011). Finally, how does the continuum of embolism avoidance vs. tolerating cycles of embolism formation and recovery relate to the continuum of leaf water potential regulation (i.e., iso vs. anisohydry; see next Section)?

C. Linking Stomatal Control of Leaf Water Potential to Xylem Functioning

A continuum exists in the degree to which stomata regulate the minimum leaf water potential. Isohydric plants represent one end of the continuum and their stomata adjust to keep the leaf water potential from dropping below a set value. Alternatively, anisohydric plants exist at the other end of the spectrum and their stomata do not act to regulate the leaf water potential at a specific value, but instead allow leaf water potential to decline as the soil dries out or the vapor pressure deficit increases. Although generalizations are often made about what types of plants exist at each end of the spectrum, a great deal of taxonomic diversity is actually observed throughout the range (Tardieu and Davies 1992; Loewenstein and Pallardy 1998a, b; Tardieu and Simonneau 1998; Bonal and Guehl 2001; West et al. 2008; Zhang et al. 2012; Pou et al. 2012). Another generalization about the spectrum is that anisohydric plants dominate arid environments. However, there are examples of species at both ends of the spectrum co-occurring in arid regions (Linton et al. 1998; McDowell et al. 2008; West et al. 2008).

There are many advantages to isohydry: the predictability of maintaining leaf water potentials at a set value (1) may keep the rest of the plant from experiencing potentially embolism-inducing xylem pressures. This could minimize construction costs of the xylem if the species depends on structural avoidance of embolism. (2) This strategy may also be associated with greater reliance on capacitance. Capacitance can be calculated as the mass of water released per unit tissue volume per change in water potential. Tissue-specific capacitance can be estimated from the slope of the initial, essentially linear portion of the tissue water release curve.

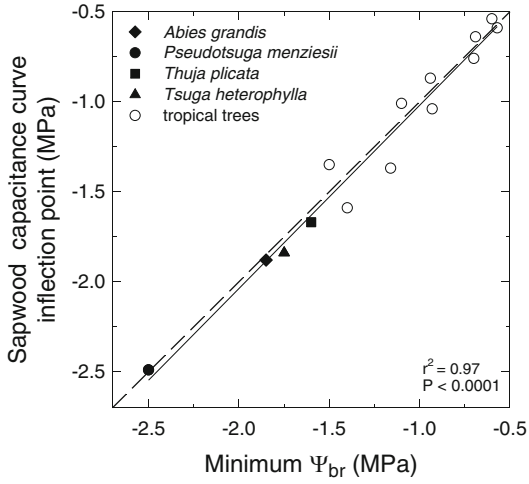

Fig. 7.6. Branch minimum water potential (Ψ_{br}) vs. the inflection point on the sapwood capacitance curve. Water potentials more negative than the inflection point experience diminished returns in terms of water released for a given drop in water potential, and these species-specific set-points for daily minimum branch water potential optimize reliance on capacitance. The data from tropical trees are from Meinzer et al. (2008a), and conifer data are from McCulloh et al. (2014)

Many plants act to maintain their leaf water potentials at milder values than the inflection point on the tissue water release curve (Fig. 7.6). (3) Furthermore, the leaves of isohydric plants would not have to undergo osmotic adjustment to maintain turgor in their living cells, which would avoid energy costs associated with solute accumulation. The obvious drawback to isohydry is that stomata must close to maintain the set leaf water potential, which prevents assimilation of new carbon. In a direct comparison of iso vs. anisohydric crops, the cost of osmotically adjusting vs. stomatal limitation on assimilation were not different (McCree and Richardson 1987), but to our knowledge this has not been examined under natural conditions.

One of the intermediaries along this continuum that has been characterized in *Eucalyptus gomphocephala* was dubbed "isohydrodynamic" (Franks et al. 2007). The stomata of these trees regulate their leaf water potentials in such a way that the pressure gradient between the soil and leaves is constant throughout the growing season. Franks et al. (2007) provided convincing evidence that the degree of stomatal regulation was adjusted based on the whole plant hydraulic conductance. This strategy has also been documented in a grapevine cultivar (Zhang et al. 2012).

There is considerable interest in determining if species at one end of the spectrum vs. the other are more likely to die during severe droughts. McDowell et al. (2008) speculate that isohydric species are more likely to die during long-term droughts because of their inability to open their stomata and capture new carbon. Species that tend to behave more anisohydrically often have more drought-resistant xylem, and this can lead to maintenance of gas exchange during mild drought stress (Pou et al. 2012). However, using a quite comprehensive dataset, Mitchell et al. (2012) showed that container-grown saplings of the more isohydric *Pinus radiata* were able to survive roughly twice as long as two more anisohydric *Eucalyptus* species during an imposed long-term drought. How these results apply to naturally growing plants is not yet clear, but is the focus of considerable current research.

III. Dynamic Responses of Tree Hydraulic Architecture

Early and ongoing research on plant hydraulic architecture have focused primarily on characterizing more or less static properties associated with specific xylem structural attributes. It is now known that constraints on photosynthetic gas exchange and growth imposed by plant hydraulic properties can be dynamic over relatively short timescales from minutes to hours. The dynamic components of hydraulic architecture present both challenges and opportunities for incorporating hydraulic traits into models that predict canopy photosynthesis. Here we discuss four dynamic phenomena whose

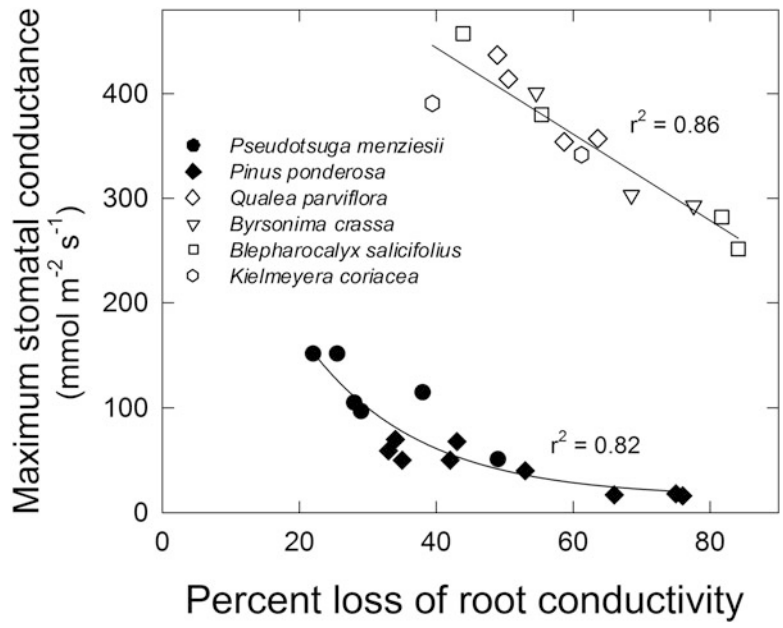

Fig. 7.7. Daily maximum stomatal conductance in relation to loss of hydraulic conductivity in shallow roots (<50 cm depth) for mature trees of two temperate coniferous species and four Brazilian savanna tree species. Data adapted from Domec et al. (2004, 2006b)

impacts on plant hydraulics are becoming increasingly well documented and understood: embolism formation and reversal, ionic effects on xylem conductance, hydraulic capacitance, and hydraulic redistribution of soil water by roots.

A. Embolism Formation and Reversal

Diurnal and seasonal cycles of embolism formation and reversal are a common source of dynamic variation in hydraulic conductance of leaves, stems and roots. Refilling of embolized xylem conduits occurs even when nearby functional conduits are still under considerable tension (McCully et al. 1998; Zwieniecki and Holbrook 1998; McCully 1999; Zwieniecki et al. 2000; Holbrook et al. 2001; Melcher et al. 2001; Bucci et al. 2003; Domec et al. 2006b; Johnson et al., 2009; Brodersen et al. 2010) implying that embolism formation and reversal are two independent, competing processes with the degree of recovery depending on the balance between the two (Bucci et al. 2003; Zwieniecki and Holbrook 2009; Nardini et al. 2011a). Daily loss and recovery of leaf hydraulic conductance has been characterized as a hydraulic circuit breaker function that triggers stomatal closure to provide an adequate safety margin for preserving the hydraulic integrity of the stem upstream (Brodribb and Holbrook 2003; Johnson et al. 2012). However, species that do not experience daily loss and recovery of leaf hydraulic function still exhibit stomatal regulation that minimizes risk of excessive embolism in stems. Although stems show formation and reversal of embolism over different time scales (Holbrook et al. 2001; Lovisolo et al. 2008; Brodersen et al. 2010; McCulloh et al. 2011a), much remains to be learned about species-specific variation in the capacity for embolism reversal in stems, especially critical levels of embolism beyond which conduit refilling does not occur (Ogasa et al. 2013). Roots are usually the most vulnerable portion of the plant hydraulic pathway and can show substantial diurnal and seasonal variation in the degree of embolism, which constrains stomatal conductance (Fig. 7.7; Domec et al. 2004, 2006b, 2009).

B. Ionic Response

The impact of certain ions, particularly K^+, on xylem conductance was apparently first noted by Zimmermann (1978) who reported

that declining flow rates of distilled water through stem segments held under a constant pressure differential could be rapidly reversed by addition of KCl to the perfusion solution. Flow rates of KCl solutions remained constant and were typically higher than initial rates observed with distilled water. These observations led to the use of dilute KCl solutions rather than distilled water as part of the standard protocol for measuring xylem hydraulic conductivity of plant segments. However, the potential significance of ionic modulation of xylem conductivity for dynamic regulation of hydraulic properties in vivo went largely unrecognized for about two decades until researchers began to systematically characterize the ionic effect in excised plant parts. They found that the ionic response is rapid, completely reversible and can result in more than a two-fold increase in xylem conductivity at higher ion concentrations and substantial increases in conductivity at concentrations representative of those in vivo (Van Ieperen et al. 2000; Zwieniecki et al. 2001; Gascò et al. 2006; Domec et al. 2007; Trifilo et al. 2008; Nardini et al. 2010, 2011b; Gortan et al. 2011; Jansen et al. 2011). The ionic effect has been attributed to the shrinkage and swelling of hydrogels in xylem vessel pit membranes (Zwieniecki et al. 2001), vessel grouping characteristics and the fraction of the vessel wall area occupied by intervessel pits (Jansen et al. 2011). Several studies have provided evidence for an ecological role of the ionic effect in intact, field grown plants. Nardini et al. (2010) observed that K^+ concentration was four times higher in xylem sap of illuminated branches than in shaded branches of *Laurus nobilis* and that this concentration difference significantly increased hydraulic conductivity of excised branches. Subsequently, Trifilo et al. (2011) reported that K^+ in xylem sap had a buffering effect on embolism-induced loss of hydraulic conductance in droughted *Laurus nobilis* plants, consistent with an earlier report of an embolism-dependent enhancement of conductivity by K^+ in three other species (Trifilo et al. 2008). The magnitude of ion-mediated enhancement of xylem conductivity may also be associated with species' ecological distributions. Nardini et al. (2012) found greater ionic enhancement of xylem conductivity in *Acer* species native to higher irradiance or lower water availability habitats than in *Acer* species from shady, humid habitats.

C. Capacitance

In addition to its buffering effect on xylem tension, hydraulic capacitance transiently increases apparent whole-tree leaf-specific hydraulic conductance through direct release of water from storage compartments into the transpiration stream, thereby partially circumventing cumulative axial resistances (Andrade et al. 1998; Meinzer et al. 2004a, 2008a). Stomatal regulation of leaf gas exchange is coordinated dynamically with transient capacitance-induced changes in apparent hydraulic conductance over the course of the day. In large tropical trees, crown conductance is highest when capacitive discharge of water into the transpiration stream is greatest and lowest when capacitance is being recharged (Fig. 7.8; Andrade et al. 1998; Meinzer et al. 2008a). This dynamic coordination of vapor and apparent liquid phase conductances in the intact plant cannot be predicted from measurements of steady state hydraulic properties on excised plant segments. Discharge and recharge of capacitance causes lags between rates of change in transpiration and stem sap flux, which can be quantified in terms of hydraulic time constants (Phillips et al. 1997, 2004; Ward et al. 2013).

The sapwood itself appears to be a major source of capacitance and sapwood capacitance on a tissue volume basis can vary dramatically among co-occurring species (e.g. Meinzer et al. 2003, 2008a, b; Scholz et al. 2007) leading to contrasting behaviors in terms of stomatal regulation of gas exchange and tree water status (Goldstein et al. 1998; Meinzer et al. 2003, 2008a). Parenchyma, fibers and the xylem conduits themselves

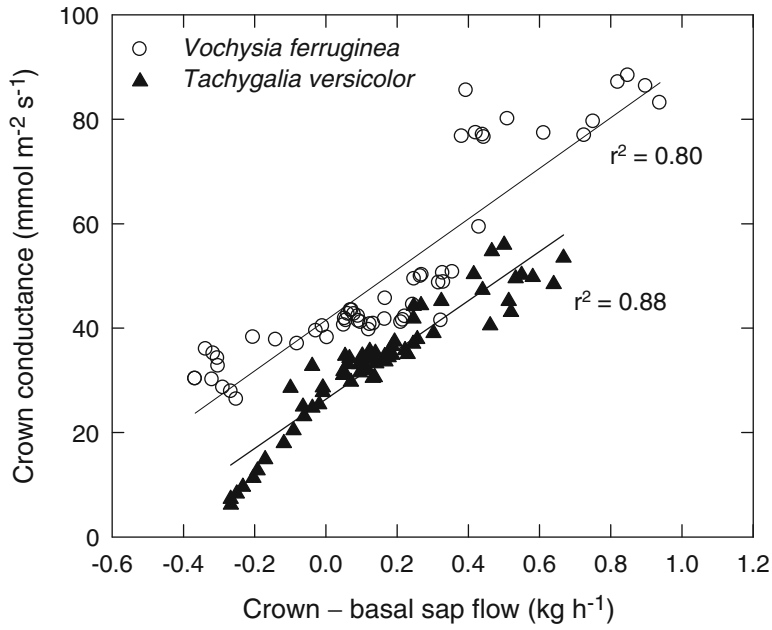

Fig. 7.8. Crown conductance estimated from branch transpiration and vapor pressure deficit in relation to daily patterns of withdrawal and recharge of internal water storage for two tropical forest canopy tree species. Positive values of crown – basal sap flow indicate withdrawal of water from storage compartments located between upper branches and the base of the trunk. Negative values indicate recharge of storage. Adapted from Meinzer et al. (2008a)

may serve as sources of sapwood capacitance (Goldstein et al. 1984; Holbrook and Sinclair 1992; Hölttä et al. 2009). Although cavitation or embolism would be required for capacitive release of water from xylem conduits, modeling exercises suggest that under a range of conditions, the positive effects on plant water status and gas exchange would outweigh the negative effects on xylem conductance, especially if conduits are refilled overnight (Hölttä et al. 2009).

D. Hydraulic Redistribution

Plant root systems passively redistribute water within the soil profile according to gradients of soil water potential. This process, commonly referred to as hydraulic redistribution (HR), can result in upward, downward and lateral movement of water from moist to drier regions of soil via the root xylem, a pathway that typically has substantially greater hydraulic conductivity than that of unsaturated soil (Neumann and Cardon 2012). The fraction of hydraulically redistributed water that passes from shallow roots into the surrounding soil can markedly reduce rates of soil drying during periods of drought (Brooks et al. 2002; Domec et al. 2004; Meinzer et al. 2004b). Additionally, hydraulically redistributed water is available for uptake by roots of neighboring plants either directly or via the soil mycorrhizal network (Querejeta et al. 2003; Plamboek et al. 2007; Warren et al. 2008). Perhaps more importantly from the standpoint of maintenance of plant hydraulic function and shoot gas exchange, the reverse flow of water from roots to soil can partially uncouple the water potential of shallow roots from that of the surrounding dry soil (Domec et al. 2004, 2006b). This phenomenon, combined with reduced rates of soil drying associated with HR, can delay the onset of drought-induced embolism, catastrophic hydraulic dysfunction and ultimately death of shallow roots. Consistent with this, the percent loss of hydraulic conductivity in shallow lateral roots of Brazilian savanna trees during the dry season decreased linearly with increasing rates of reverse sap flow in those roots (Scholz et al. 2008) and internal hydraulic redistribution in *Vitis* root systems has been shown to prolong root lifespan (Bauerle et al. 2008). Thus, given the relatively small

quantities of water redistributed from moist to drier soil via HR (Meinzer et al. 2004b; Warren et al. 2007), the direct contribution of hydraulically redistributed water to maintenance of transpiration during dry periods is likely to be marginal compared to the impact of internal HR on maintenance of root hydraulic function. Because shallow roots and the aerial portion of the plant act as competing sinks for water taken up by deeper roots in moist soil, processes such as nocturnal transpiration inhibit HR (Howard et al. 2009) with potential negative consequences for functioning and survival of shallow roots during dry periods. If warmer nights and higher vapor pressure deficits predicted under future climate regimes enhance nocturnal transpiration or delay nocturnal rehydration of the aerial portion of the plant, the mitigation of drought-induced root embolism by HR is likely to be impaired.

IV. Environmental Plasticity

Numerous studies have documented trends in various components of hydraulic architecture along gradients of aerial and belowground environmental variables. Most of these studies involve comparisons of selected hydraulic traits of multiple species representative of contrasting vegetation types, whereas relatively few have focused on intraspecific trends across broad environmental gradients. In single species studies, the relative roles of genetic versus environmental determinants of hydraulic traits may be unclear unless work has been carried out under a common garden design. Another constraint on interpretation of environmental trends in hydraulic architecture arises when comparisons are based on individual traits from excised plant segments. Inferences drawn from patterns of variation traits such as P_{50} of terminal branches may be limited because selection for suites of hydraulic traits that confer adequate plant fitness under given conditions is likely to occur at the organismal level (Meinzer et al. 2010). Here we discuss selected examples of variation in hydraulic architecture along gradients of aridity, temperature, soil texture and nutrient availability.

A. Aridity

Aridity is expected to be a key determinant of the hydraulic architecture of woody perennials. Consistent with this, in a study of 167 species representing five vegetation types Maherali et al. (2004) found that P_{50} of branch segments ranged from a median value of about −5.3 MPa in Mediterranean climates species to only −0.8 MPa in tropical rainforest species. At the individual species level, a common garden study of *Pseudotsuga menziesii* seedlings from coastal and interior wet and dry climates found that both roots and shoots tended to be more resistant to embolism in populations from dry sites (Kavanagh et al. 1999). However, other studies of hydraulic adjustments of individual species across aridity gradients suggest that maintenance of integrity of water transport and homeostasis of leaf level gas exchange in mature, field-grown trees may be attained largely via changes in tree allometry. A survey of hydraulic traits of *Pinus sylvestris* across a gradient of climate dryness in Europe yielded no significant trend in branch P_{50}, but significant trends of decreasing branch level leaf area to sapwood area ratio (A_L:A_S) and increasing leaf specific conductivity (k_L) with increasing dryness (Martinez-Vilalta et al. 2009). Thus, shifts in branch allometry that resulted in increased k_L apparently compensated for the tendency for xylem tension to increase with aridity. Similarly, tree allometric adjustments in *Pinus palustris* resulted in homeostasis of whole-tree leaf-specific hydraulic conductance and stomatal control of gas exchange in trees growing xeric and mesic sites (Addington et al. 2006). Allometric trends in *Pinus ponderosa* trees caused whole-tree k_L and canopy conductance to be substantially greater in desert populations than in montane populations (Maherali and DeLucia 2001).

B. Freezing

Climatic gradients of increasing frequency and severity of freezing temperatures imply an increased risk of disruption of water transport from freeze-thaw-induced embolism (see section two above), especially in overwintering evergreen species. Xylem vulnerability to freeze-thaw-induced embolism increases with conduit diameter (Davis et al. 1999; Pittermann and Sperry 2003), yet many species growing in frost-prone climates have xylem conduits large enough to experience freezing induced embolism and consequent reduction of water transport capacity probably because smaller conduits would unduly restrict water transport and gas exchange (Davis et al. 1999). The effects of freezing-induced embolism can be overcome by production of new xylem conduits in the spring as in winter-deciduous species or refilling of conduits during periods of above-freezing temperatures as in many evergreen species (Mayr et al. 2006; McCulloh et al. 2011a, b). Nevertheless, if freezing temperatures are low enough, embolism will spread to progressively smaller conduits and become essentially irreversible resulting in plant mortality. Relationships between xylem vulnerability to and capacity for recovery from freezing-induced embolism are likely to be important determinants of latitudinal (Pockman and Sperry 1997) and altitudinal (Feild and Brodribb 2001; Choat et al. 2011) distributions of species. In drought-prone climates with freezing temperatures, drought hardening can contribute to avoidance of freezing-induced loss of hydraulic function (Medeiros and Pockman 2011).

C. Soil Texture

Soil texture and its impact on pore size distribution are major determinants of the moisture releasing characteristics of soils (Brooks and Corey 1964; Warren et al. 2005). It is not surprising therefore, that plants would exhibit a range of structural and physiological features that optimize soil water extraction along gradients of soil texture independent of gradients in other environmental variables such as aridity (Sperry et al. 1998). In a study of *Pinus taeda* growing in a loamy versus sandy soil, Hacke et al. (2000) found that trees growing in sandy soil had substantially higher root area to leaf area ratios, were more deeply rooted, and were more vulnerable to xylem embolism than trees growing in a loamy soil with its much higher clay fraction. Structural and physiological adjustments in both soil types served to maintain soil water extraction at about 86 % of its potential value in both soils. Populations of *Pinus ponderosa* and *Pseudotsuga menziesii* growing in sites with a semi-arid continental climate east of the Cascade Mountains had trunk sapwood with higher specific hydraulic conductivity, higher capacitance and greater vulnerability to embolism than sapwood of the same species growing in sites with a moist maritime climate west of the mountains (Barnard et al. 2011). This somewhat counter-intuitive pattern was attributed to greater soil porosity in the semi-arid sites where about 90 % of the available water is extracted over a relatively narrow range of soil water potential, suggesting little selective pressure for xylem structural reinforcements that would allow greater xylem tension to be sustained without increased risk of embolism. In contrast, the finer textured soils in the maritime climate sites show a broader range of water potential over which it would be physiologically feasible to extract water through xylem structural adjustments that enhance resistance to embolism.

D. Nutrient Availability

The availability of nutrients, particularly N and P can have pronounced effects on tree hydraulic architecture and photosynthetic gas exchange mediated by adjustments in both tree allometry and in the structure and properties of the xylem. Five years of N fertilization in a Brazilian savanna ecosystem resulted in increased whole-tree leaf areas and leaf area to sapwood area ratios

among five dominant species differing in leaf phenology (Bucci et al. 2006). Despite their increased leaf area, whole-tree transpiration was not significantly greater in N-fertilized trees because stomatal conductance on a unit leaf area basis was significantly lower. Adjustments in sapwood hydraulic and biophysical properties induced by N fertilization included higher xylem specific conductivity, more negative values of P_{50} and lower wood density. This combination of sapwood traits was not consistent with frequently observed trade-offs of hydraulic safety against efficiency (see above) or with some reported relationships between wood density and xylem vulnerability to embolism (Hacke et al. 2001). Despite higher sapwood specific conductivity in N-fertilized trees, their daily minimum values of leaf water potential were significantly lower, probably as a result of higher leaf area to sapwood area ratios and lower root to shoot ratios. In *Pinus taeda* trees, increased growth rates in an N fertilization treatment were associated with greater stand leaf area index, but lower root to leaf area ratios, lower leaf-specific hydraulic conductance and lower values of reference stomatal conductance (Ewers et al. 2000). In dwarf stands of the mangrove *Rhizophora mangle*, growth rates of trees fertilized with N were several times higher than in unfertilized trees, but rates of photosynthesis and stomatal conductance were similar to those in unfertilized trees (Lovelock et al. 2004). Taken together, the preceding observations suggest that growth enhancement by N fertilization may often be the result of adjustments in hydraulic architecture that allow increases in whole-crown photosynthesis with increasing leaf area rather than increased rates of photosynthesis per unit leaf area.

V. Scaling from Leaf to Canopy

Stomatal regulation of photosynthetic gas exchange at the leaf level is a manifestation of dynamic coordination between vapor and liquid phase conductances, particularly apparent K_L, which represents the integration of static properties and dynamic processes along the plant hydraulic continuum. Therefore, the role of tree hydraulics in regulation of stomatal behavior and photosynthesis cannot be fully understood unless hydraulic properties and dynamic processes are studied over a range of scale at various points along the root-to-leaf continuum. Scaling of stomatal conductance and photosynthesis with k_L is often strikingly similar among co-occurring species (Fig. 7.9; Meinzer et al. 1995; Brodribb and Feild 2000; Santiago et al. 2004).

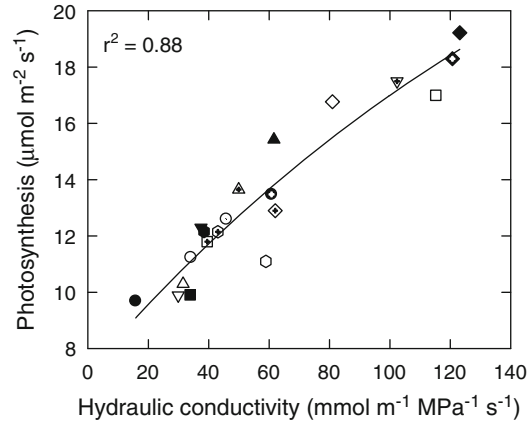

Fig. 7.9. Daily maximum rates of photosynthesis in relation to maximum leaf-specific conductivity in upper branches of 20 Panamanian forest canopy tree species. Adapted from Santiago et al. (2004)

The specific signals involved in stomatal responses to variation in k_L are unclear. Much work has focused on leaf water potential as a physiological set-point for stomatal regulation of gas exchange. However, there is increasing evidence that stomatal regulation of transpiration is coordinated with species-specific set-points for minimum stem water potential such that a relatively constant hydraulic safety margin is maintained in terminal branches (Jones and Sutherland 1991; Sparks and Black 1999; Meinzer et al. 2008a; 2009; Choat et al. 2012; Johnson et al. 2012; Zhang et al. 2013). There is also evidence that diurnal fluctuations in leaf hydraulic capacity are

involved (Brodribb and Holbrook 2003; Bucci et al. 2003; Johnson et al. 2009, 2011).

A. Dynamic Scaling Relationships

Strictly speaking, k_L refers to fixed properties of the hydraulic pathway observed under steady state conditions. However, a number of processes operating at different temporal and spatial scales can cause dynamic variation in apparent k_L leading to adjustments in stomatal control of gas exchange. As described above, daily time courses of crown level stomatal conductance are coordinated with discharge and recharge of capacitance, which transiently influences whole-tree apparent k_L (Fig. 7.8; Andrade et al. 1998; Meinzer et al. 2008a) and species with higher intrinsic sapwood capacitance tend to have higher whole-tree hydraulic conductance estimated under quasi-steady state conditions (Meinzer et al. 2003; Scholz et al. 2007). Stomatal conductance of fully illuminated leaves can also increase rapidly in response to reductions in transpiring leaf area resulting from events such as partial shading (Whitehead et al. 1996) and defoliation (Pataki et al. 1998) of portions of tree crowns, presumably because of concomitant increases in whole-tree k_L. An extreme example of stomatal responses to changes in the ratio of leaf area to hydraulic capacity would be high rates of gas exchange observed in new leaves of recently coppiced trees (Tschaplinski and Blake 1989).

B. Impacts of Tree Size

As trees increase in height, stomatal conductance and photosynthesis are increasingly constrained by frictional resistances associated with path-length and gravitational effects on xylem tension. Although path-length resistances can be partially compensated by increases in trunk xylem specific conductivity (Domec and Gartner 2003) and reductions in the leaf area to sapwood area ratio (McDowell et al. 2002), height-related changes in the gravitational component of xylem tension (0.01 MPa m^{-1}) are inescapable and therefore not an inherently hydraulic influence. Compensatory adjustments in hydraulic architecture can to some extent mitigate the impact of increasing height on photosynthetic gas exchange. Nevertheless, maximum tree height may be ultimately limited by unavoidable conflicts between increased resistance to tension-induced embolism and decreasing hydraulic conductivity in terminal branches (Domec et al. 2008).

Measurements of height-related trends in whole-tree k_L appear to be relatively rare, but the available literature suggests that the relative decline in k_L with increasing height varies dramatically among species. Ryan et al. (2000) reported a 50 % decline in k_L of *Pinus ponderosa* trees over a 24 m height increase from 12 to 36 m, whereas McDowell et al. (2002) found a 50 % decline in k_L of *Pseudotsuga menziesii* trees with a 45 m height increase from 15 to 60 m but with a decline of less than 10 % between height classes of 32 and 60 m. Changes in hydraulic architecture with increasing tree size can also be considerably more abrupt. Specific conductivity of branch xylem decreased by more than 50 % between mean height classes of 4.6 and 9 m in the tropical savanna tree *Sclerolobium paniculatum* (Zhang et al. 2009). This was partially compensated by a decline in branch leaf area to sapwood area ratio such that leaf-specific conductivity declined by only 25 %, but at the cost of reduced photosynthetic leaf area in relation to carbon allocated to branch wood. As expected, height-related declines in k_L are associated with corresponding declines in stomatal conductance and transpiration that modulate vertical gradients of leaf water potential (Niinemets 2002).

Height-related changes in foliar stable carbon isotope composition have been used as an integrated measure of hydraulic constraints on photosynthetic gas exchange. Carbon isotope discrimination of fully illuminated foliage typically decreases with increasing height consistent with increasing relative stomatal limitation of photosynthesis (Koch et al. 2004; Martinez-Vilalta et al. 2007;

Ambrose et al. 2009). However, mesophyll conductance also decreases with increasing height (Woodruff et al. 2008), implying that the height-related decline in carbon isotope discrimination is likely to result from the combined influence of dynamic hydraulic constraints on stomatal conductance and leaf structural constraints on CO_2 diffusion (Niinemets 2002; Ishii et al. 2008; Woodruff et al. 2008).

C. Tree to Stand Scaling

Coordinated adjustments in tree hydraulic architecture and stomatal control of gas exchange are observable at the stand level and often result in partial or complete homeostasis of certain functional attributes across scales. Following thinning treatments that resulted in a five-fold difference in spacing among *Pinus sylvestris* trees in two adjacent plots, differences in stomatal and canopy conductance and canopy transpiration were less than twofold and leaf water potential was nearly identical in the two plots (Whitehead et al. 1984). Seasonal adjustments in canopy conductance and leaf area in Brazilian savanna sites caused canopy transpiration to be similar between the dry and wet seasons despite substantially greater atmospheric vapor pressure deficits during the dry season (Bucci et al. 2008). Coordinated adjustments in tree hydraulic architecture and stomatal control of transpiration have been shown to result in a high degree of homeostasis of minimum leaf water potential among stands of different ages (Ewers et al. 2007b), stands experiencing different levels of water availability (Fisher et al. 2006) and stands experiencing interannual climate variation (Ewers et al. 2007a).

D. Simple Biophysical and Architectural Proxies for Scaling

Simple biophysical and architectural traits of trees can often be used as proxies for more difficult to characterize hydraulic architectural traits that influence photosynthetic gas exchange. Among the simplest of these traits is wood density, which can serve as a proxy for xylem specific conductivity because wood density reflects the relative volumes of solid material and xylem conduits responsible for water transport. Thus conductivity would be expected to decrease with increasing wood density. Dense ring-porous wood is a potential exception because the presence of relatively few large vessels could compensate for the impact of a dense fiber matrix. Functional traits that have been shown to scale uniformly with wood density among co-occurring species include xylem specific conductivity and k_L (Bucci et al. 2004, 2009; Meinzer et al. 2008b), minimum leaf water potential (Bucci et al. 2004, 2009), sapwood hydraulic capacitance (Scholz et al. 2007; Meinzer et al. 2008b), maximum photosynthetic rate (Santiago et al. 2004), total daily transpiration per unit leaf area (Bucci et al. 2004) and whole-tree k_L (McCulloh et al. 2011a, b). Although sapwood capacitance has been reported to scale uniformly with wood density among co-occurring species, scaling relationships between capacitance and wood density appear to vary across sites (Scholz et al. 2007; Meinzer et al. 2008b). Positive correlations between wood density and xylem resistance to embolism are frequently (Hacke et al. 2001; Pratt et al. 2007) but not always (Bucci et al. 2006) observed.

VI. Conclusions

The inextricable links between water use, carbon gain and survival of plants means that to understand plant responses to environmental and competitive pressures one needs a comprehensive understanding of the mechanisms that plants have developed to maximize water transport capacity and to minimize vulnerability to hydraulic failure; as well as the trade-offs involved in balancing these two necessities. Understanding these mechanisms and traits is particularly important when attempting to predict how ecosystems will respond to changes in climate, or to expanding human activities and

land use. The responses of plants to climate extremes, for example, vary from one species to another depending on the different combinations of traits that species possess to cope with these pressures. Although substantial progress has been made in characterizing plant responses to environmental parameters across a range of scales, current models have fallen short in their ability to accurately predict responses to climate extremes. The recent wide-scale drought-induced mortality of piñon pine, and the relatively limited mortality of juniper in the southwest United States (up to 95 and 25 % mortality for piñon and juniper, respectively; Breshears et al. 2005), for example, would not have been predicted with current models such as those which are parameterized by plant functional type (i.e. evergreen needle-leaf forests). Because the two species which exhibit very different strategies in response to climate extremes are indistinguishable within the plant functional type concept, an improved functional trait-based approach is needed that can more effectively describe specific plant adaptive strategies in response to competition and stressors. We believe that the development and application of models that effectively incorporate the hydraulic mechanisms and traits described in this chapter (plus those which have yet to be characterized) will represent a substantial advancement in our ability to more accurately predict plant responses to environmental and competitive stressors.

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