Chapter 9
Wood Anatomy and Plant Hydraulics in a Changing Climate

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1 Introduction

Due to their hydraulic system that allows them to transport water from the soil to leaves, woody plants have become incredibly successful in terrestrial ecosystems since their evolution ~400 million years ago (Hartmann 2011). This vascular system lets trees conduct water from the soil up to more than 100 m (Koch et al. 2004), allowing trees to compete for light and absorb several petagrams of carbon from the atmosphere via photosynthesis every year (Le Quéré et al. 2009). Thus, plant hydraulics form the "backbone" of most terrestrial ecosystems, facilitating net primary production and carbon sequestration by the biosphere (Brodribb 2009). The carbon sequestration of global forests alone is estimated at roughly 2.5 Pg carbon, equivalent to 25 % of anthropogenic carbon emissions in 2010 (Pan et al. 2011). Similarly, vascular transport plays a major role in the global hydrological water recycling that drives upwards of 80 % of evapotranspiration over land, influencing global circulation and precipitation patterns (Jasechko et al. 2013).

Hydraulic architecture comprises part of an integrated set of traits and life history trade-offs that allow woody plants to colonize diverse environments, compete, and coexist. Wood anatomy plays a central role in plant hydraulic strategies due to the inherent trade-offs associated with partitioning of wood volume between water transport and structural support functions and a fixed pool of carbon and energy that can be allocated across growth, fecundity, tissue maintenance, and tissue repair (Chave et al. 2009; Domec et al. 2008). Maximizing fitness is thought to involve

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maximum carbon uptake for growth and reproduction, which requires water transport to the canopy, while avoiding the damaging or lethal risks of abiotic stressors such as water limitation and mechanical damage (Chave et al. 2009; Cowan 1978). Wood anatomy interacts with other components in the hydraulic continuum, including the root–rhizosphere interface and the water–air interface in stomatal pores on leaves (Barnard et al. 2011). Furthermore, the allocation to different tissues, including sapwood, fine roots, leaves, as well as rooting distribution and depth, are other major components of individuals' and species' hydraulic strategies.

Wood anatomy and plant hydraulics will be central in understanding species' responses to and ability to cope with rapid environmental change, including anthropogenic climate change (McDowell et al. 2008). While plant hydraulics have evolved to changes in climate over evolutionary timescales (Pittermann et al. 2012), the recent and future rates of climate change are likely to place considerable stress on vascular plants. Global temperatures have increased roughly 0.8 °C since preindustrial times (IPCC 2013), but the rate of temperature increase over 1980–2005 was faster than that of any documented rapid warming period in the geologic past, including warming periods that triggered mass extinctions (Diffenbaugh and Field 2013). The projected magnitude of warming approaches those of the geologic record, but with 10–50-fold faster rates (Diffenbaugh and Field 2013). Due to rising temperatures, an "acceleration" of the hydrological cycle is also expected, leading to wet areas generally getting wetter and dry areas generally getting drier (Betts et al. 2007). Similarly, projections indicate that longer dry spells and increased evaporative demand due to higher temperatures will increase drought stress in many regions of the world, particularly in tropical South America, southern Europe, Australia, western United States, and subtropic Africa (Dai 2013) (Fig. 9.1). Rising atmospheric carbon dioxide concentrations, however, may help trees ameliorate drought stress due to increasing water use efficiency (Keenan et al. 2013), and consequently the balance of these trends is largely unknown (Bonan 2008; Friend et al. 2013).

Though no global datasets currently exist to assess temporal trends, widespread tree mortality triggered by drought and heat stress has been observed on every vegetated continent in recent decades (Allen et al. 2010; Anderegg et al. 2013b) (Fig. 9.2). Some of these events have included regional-scale massive die-offs, such as the mortality of *Pinus edulis* and *Populus tremuloides*, in the western United States following abnormally hot droughts in 2000–2003 (Anderegg et al. 2012b; Breshears et al. 2005; Worrall et al. 2008). Where temporal data are available, plot networks monitored from the 1960s to present indicate that background mortality rates in western North America have increased substantially over that period, likely due to climate stress (Peng et al. 2011; van Mantgem et al. 2009). Due in large part to major uncertainties surrounding how trees die from drought stress, current predictive ability of which species are most vulnerable, when, where, and to what types of drought is very limited (Anderegg et al. 2012a; McDowell et al. 2011).

Plant hydraulics and wood anatomy are likely important traits in assessing species' vulnerability to increasing severity of climatic stresses, such as drought, high temperatures, and consequent high evaporative demand. The biophysical properties

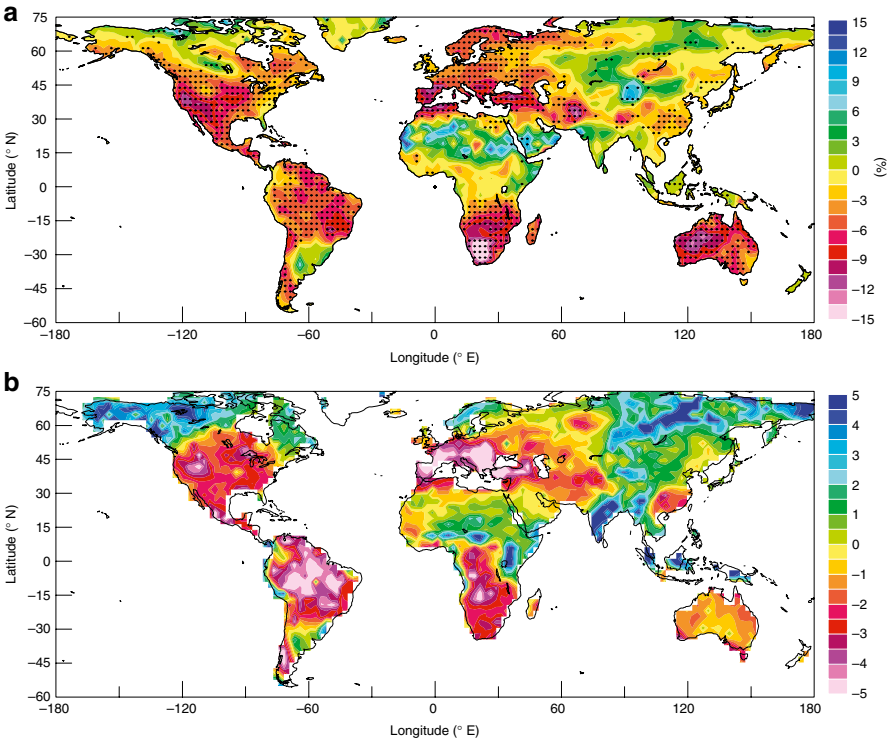

Fig. 9.1 (**a**) Percentage changes from 1980–1999 to 2080–2099 in the multimodel ensemble mean soil-moisture content in the top 10 cm layer (broadly similar for the whole soil layer) simulated by 11 CMIP5 models under the RCP4. Five emissions scenario. Stippling indicates at least 82 % (9 out of 11) of the models agree on the sign of change. (**b**) Mean self-calibrated Palmer Drought Severity Index using the Penman-Monteith formulation (sc_PDSI_pm) averaged over 2090–2099 computed using the 14-model ensemble mean climate (including surface air temperature, precipitation, wind speed, specific humidity, and net radiation) from the CMIP5 simulations under the RCP4.5 scenario. A sc_PDSI_pm value of −3.0 or below indicates severe to extreme droughts for the present climate. Adapted from Dai (2013)

of wood and the structure and configuration of the xylem conduits contained therein are key determinants of the efficiency of whole-plant water transport, resistance to hydraulic dysfunction, and recovery of water transport capacity following periods of hydraulic dysfunction (Tyree and Zimmermann 2002). The structural features that govern the efficiency and safety of water transport at the individual conduit level are discussed in detail elsewhere in this volume. Briefly, the hydraulic conductivity of coniferous tracheids is largely determined by the size and frequency of their bordered pits, the pit membrane pore size, as well as tracheid diameter (Domec et al. 2006; Hacke et al. 2004; Pittermann et al. 2005, 2010), whereas conductivity of angiosperm vessels is most strongly related to their diameter and length (Sperry et al. 2006; Zanne et al. 2010). Conduit hydraulic safety or resistance to embolism is most strongly related to pit membrane pore size in vessels and to bordered pit

Fig. 9.2 Images of climate-induced forest die-off from around the world, adapted from Anderegg et al. (2013b). Photo credits, clock-wise from *top left*: Spain—Rafael Navarro-Cerrillo, China—Youquing Luo, New Mexico—Craig D. Allen, Argentina—Thomas Kitzberger

characteristics, particularly torus overlap at the pit aperture and margo pore size near the torus edge in tracheids (Delzon et al. 2010; Domec et al. 2006, 2008; Hacke and Jansen 2009; Hacke et al. 2004). A third biophysical property of wood related to its structure is hydraulic capacitance, the amount of water released per unit decline in water potential or increase in xylem tension. Capacitive discharge of water into the transpiration stream during the day and recharge of capacitance overnight can play an important role in buffering transpiration-induced fluctuations in xylem tension that could lead to catastrophic levels of embolism in the absence of transient buffering (Hölttä et al. 2009; Meinzer et al. 2003, 2008a, 2009). As might be expected, capacitance is inversely related to wood density (McCulloh et al. 2014; Scholz et al. 2008), which reflects the relative volumes of solid material and pore space available for water storage in wood. Not surprisingly, all of the preceding wood structural features and biophysical properties exhibit strong axial variation from woody roots to terminal branches associated with corresponding axial trends of increasing xylem tension (Domec et al. 2008; Koch et al. 2004; Woodruff et al. 2004). In tall conifers, wood features such as tracheid diameter, specific conductivity, and P_{50} vary dramatically across two orders of magnitude of stem diameter from the trunk base to terminal branches, which can correspond to a height range and path length of >50 m (Fig. 9.3). Thus, the degree of plasticity of wood structure and function

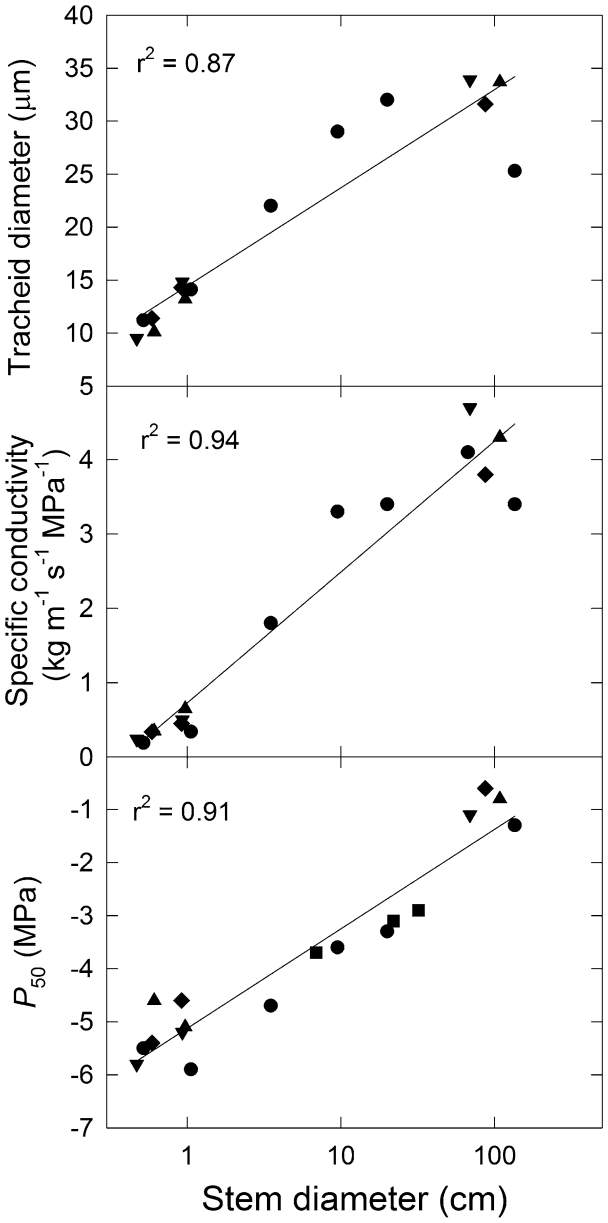

Fig. 9.3 Axial variation in stem anatomical and hydraulic properties in several tall coniferous species. Axial positions range from the trunk base to terminal branches >50 m above the ground. Symbols: (*inverted filled triangle*) *Abies grandis*; (*filled triangle*) *Thuja plicata*; (*filled square*) *Pinus ponderosa*; (*filled diamond*) *Tsuga heterophylla*; (*filled circle*) *Pseudotsuga menziesii*. Note log scale on *x*-axis. Data from Domec and Gartner (2001, 2003); Domec et al. (2006), McCulloh et al. (2014)

within individual plants may serve as a suitable proxy for a species' ability to maintain the integrity of xylem water transport in the face of climate-induced alterations in baseline levels and extremes of xylem tension.

In this chapter, we first provide an overview of the trade-offs present in wood anatomy and physiology by woody plants. We then discuss how rising carbon dioxide concentrations, increasing temperature, and more severe droughts may alter wood anatomy and plant hydraulics and conversely how these plant traits can help predict cross-species vulnerability to climatic changes. We further examine the breadth and potential for anatomical plasticity and its relationship with measured hydraulic properties. We conclude with prominent future research directions and major gaps in the understanding of plant anatomy, physiology, and demography in a world of rapid environmental change.

2 Trade-Offs in Wood Anatomy and Physiology

Species exhibit different operating ranges along continua of wood properties that determine higher order plant hydraulic traits and physiological behavior that conserves hydraulic function. Typically, the trajectory of one wood structural feature or biophysical property dictates the trajectories of other related biophysical, hydraulic and physiological traits and behaviors, resulting in a series of trade-offs. These hydraulic trade-offs are components of overall species strategies for acquisition of other resources in addition to water (Reich 2014). The classic hydraulic trade-off is one of xylem safety versus efficiency, wherein more conductive xylem is less resistant to drought-induced embolism (Meinzer et al. 2010; Sperry et al. 2008; Tyree et al. 1994). As explained above, capacitance can play a central role in avoidance of tension-induced embolism under nonextreme diurnal conditions. However, there appears to be a trade-off of capacitance against resistance to drought-induced embolism across a broad range of woody species (Fig. 9.4). The trade-off is nonlinear and characterized by a threshold lower limit of capacitance below which resistance to embolism increases sharply as capacitance declines. The relationship between capacitance and P_{50} may reflect the rapidly diminishing transient buffering effect of capacitance on xylem tension under conditions of progressively intensifying drought that prevent overnight recharge of tissue water storage compartments. This potential limitation could be partially mitigated if embolism were more readily reversible in species with high capacitance, but this remains to be elucidated.

Wood density is a fundamental biophysical property that can often serve as a robust proxy for an array of simple and complex hydraulic traits over a range of scale from tissue to whole plants (Chave et al. 2009; Meinzer et al. 2008a; Pratt et al. 2007; Zanne et al. 2010). In tropical trees, traits such as trunk-to-branch tapering of vessels, branch leaf-specific conductivity, and whole-plant leaf-specific conductance have been shown to be strongly related to wood density (Fig. 9.5). These and other hydraulic traits often scale uniformly with wood density across species and functional types such as pioneer (low density) and late successional

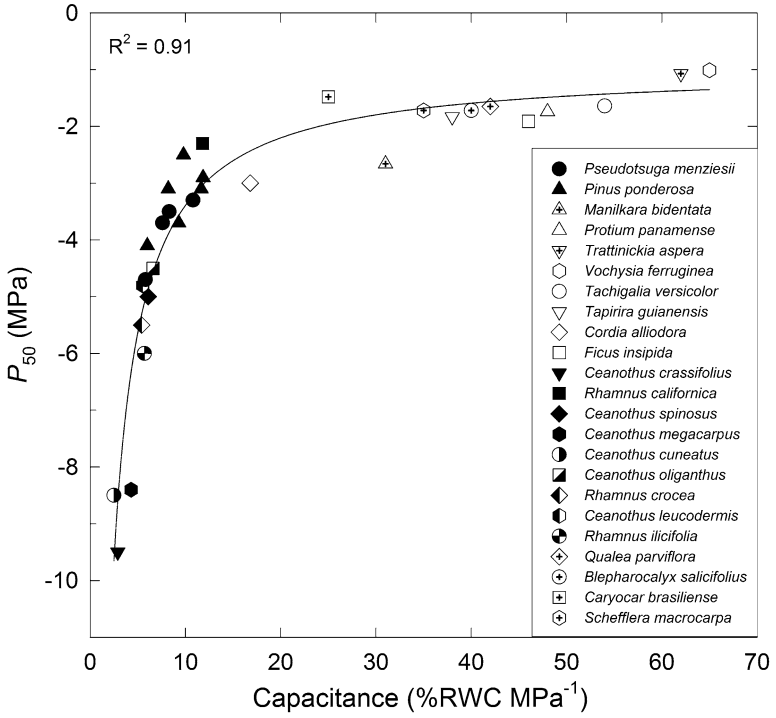

Fig. 9.4 Relationship between sapwood capacitance and the xylem pressure causing 50 % loss of stem conductivity (P_{50}) for several conifer and angiosperm tree species from different ecosystems. Figure from Scholz et al. (2011)

(high density) species (Fig. 9.5). Additional relationships between hydraulic traits and wood density include a positive correlation with resistance to embolism (Bucci et al. 2013; Hacke et al. 2001a; Ogasa et al. 2013; Pratt et al. 2007), a negative correlation with sapwood capacitance (Meinzer et al. 2008b; Scholz et al. 2011), and a negative correlation with minimum leaf water potential and leaf water potential at turgor loss (Meinzer 2003; Meinzer et al. 2008b).

Hydraulic safety margins are an example of higher order physiological regulation associated with basic wood anatomical and biophysical properties. A hydraulic safety margin can be defined as the difference between a given point along a plant organ's xylem vulnerability curve (e.g., P_{50}) and the organ's normal daily minimum xylem pressure determined by stomatal regulation of transpiration (Brodribb et al. 2003; Bucci et al. 2013; Jones and Sutherland 1991; Meinzer et al. 2009; Sparks and Black 1999; Tyree and Sperry 1988). Multispecies plots of branch P_{50} against minimum branch water potential (an estimate of xylem pressure) reveal that safety margins increase as minimum water potential becomes more negative (Pockman and Sperry 2000) and that the tracheid-bearing conifers tend to sustain more negative branch water potentials and maintain larger hydraulic safety margins than the

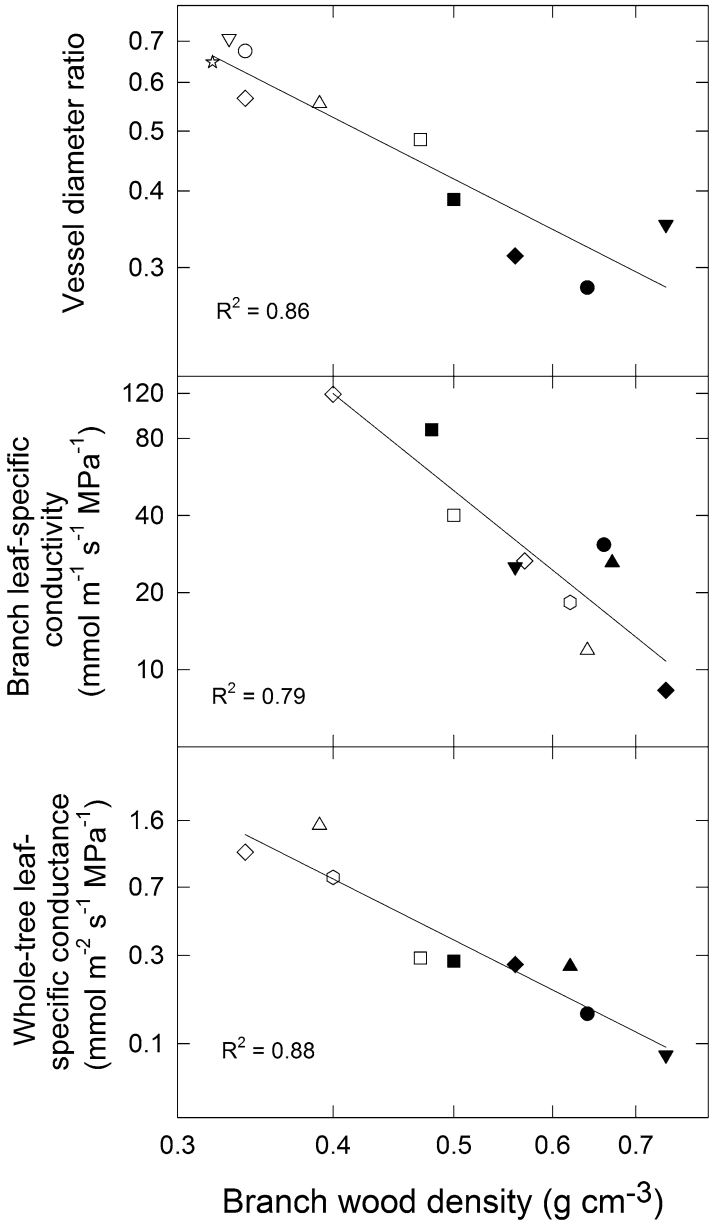

Fig. 9.5 Relationships between branch to trunk vessel diameter ratio (axial tapering), branch leaf-specific conductivity, and whole-tree leaf specific conductance and branch wood density for several Panamanian forest canopy tree species. Each symbol represents a different species. *Open symbols* correspond to early successional (pioneer) species and *closed symbols* correspond to late successional species. Note log scales on all axes. Data from Meinzer et al. (2008a) and McCulloh et al. (2011)

vessel-bearing angiosperms (Choat et al. 2012; Meinzer et al. 2009). Moreover, when safety margins are referenced to the air entry threshold, the inflection point on the xylem vulnerability curve at which loss of conductivity begins to increase steeply with decreasing xylem pressure, many angiosperms exhibit slightly negative safety margins implying that they may normally experience low baseline levels of embolism (Meinzer et al. 2009). These patterns have led to the suggestion that angiosperm trees operate perilously close to their limits for catastrophic hydraulic failure and are at a high risk of mortality during drought events (Choat et al. 2012). However, accumulating evidence points to a robust capacity of many angiosperms to regain stem hydraulic capacity following large drought-induced losses (Martorell et al. 2014; Ogasa et al. 2013; Urli et al. 2013). In contrast, conifers are reputed to have a low ability to recover from massive embolism, consistent with their maintenance of larger safety margins (Brodribb et al. 2010; Brodribb and Cochard 2009). The tendency for conifers to operate at larger hydraulic safety margins than angiosperms is also correlated with lower volume fractions of xylem parenchyma in conifer than in angiosperm sapwood (Johnson et al. 2012). These differences in xylem parenchyma volume are also correlated with higher nonstructural carbohydrate concentrations in angiosperm wood, which has led to the hypothesis that sugars may play a more important role in embolism reversal (Bucci et al. 2003; Salleo et al. 2009) in angiosperms than conifers, reducing the risk of angiosperms operating at smaller hydraulic safety margins (Johnson et al. 2012).

Despite strong relationships between wood anatomy and a series of hydraulic traits, using these traits to reliably predict differences in species performance and survival under current and anticipated climate scenarios remains somewhat elusive. It seems clear that individual traits such as stem P_{50} are not sufficient because surveys of variation in P_{50} within different vegetation types (e.g., Maherali et al. 2004) and among co-occurring species (e.g., Jacobsen et al. 2007; Pratt et al. 2012) indicate that multiple plant hydraulic strategies can be successful in a given environment. Thus, in addition to the hydraulic traits and trade-offs that can be characterized based on wood and conduit structure, plant architectural and behavioral attributes such as rooting depth, degree of iso- or anisohydry, and phenology will likely need to be taken into account.

3 Wood Anatomy, Physiology, and Global Change Drivers

Since preindustrial times (ca. 1750), atmospheric CO_2 concentrations have risen from 280 parts per million to around 400 parts per million in 2013. Rising CO_2 concentrations has generally increased water use efficiency of forests (Keenan et al. 2013), allowing them to take up more carbon per unit water, and possibly buffer water stress as well (Ponce Campos et al. 2013). Elevated CO_2 concentrations have been documented to affect xylem anatomy, leading to generally larger conduit sizes in ring-porous angiosperm species and some gymnosperms, but little changes in conduit sizes in diffuse-porous angiosperm species (Domec et al. 2010; Phillips

et al. 2011; Way 2013). Because increases in conduit size largely increase hydraulic conductivity, this can lead to higher vulnerability to water stress, but the interactive effects of CO_2 concentrations with concomitant rises in temperature and drought regimes may offset or counter these patterns (Kilpeläinen et al. 2007; Maherali and DeLucia 2000a).

Similarly, rising temperatures will also affect xylem anatomy and physiology. In a 6-year growth chamber experiment in *Pinus sylvestris*, elevated temperatures differentially affected xylem anatomy more than elevated CO_2 concentrations, leading to increases in tracheid width, length, and coarseness, and the effects were most pronounced in early wood (Kilpeläinen et al. 2007). In *Eucalyptus camaldulensis*, however, growth at higher temperatures led to higher wood density, lower hydraulic conductance, and a shift toward smaller vessel diameters (Thomas et al. 2004). Temperature can affect hydraulic vulnerability to cavitation, both through effects on conduit size and xylem anatomy and through effects on xylem fluid viscosity, although most of the evidence for this comes from studies of contrasting existing environments (e.g., Maherali and DeLucia 2000b).

Naturally, water availability places the largest constraints on xylem anatomy and physiology. Vulnerability to cavitation shows remarkable adaptive radiation across environments, differing widely as a function of water limitation across species (Maherali et al. 2004). Similarly, over evolutionary timescales, dry periods have been shown to drive the adaptation of cavitation-resistant xylem across the hydraulically diverse Cupressaceae family at multiple points in the past 30 million years (Pittermann et al. 2012).

The tight coupling between xylem anatomy, function, and the environment indicates that hydraulic characteristics and traits can provide useful insights into which species, biomes, and locations could be most vulnerable to drought (Nardini et al. 2013). Lethal failure of the plant hydraulic system has been observed in a number of species in response to drought (Anderegg et al. 2012b; Brodribb and Cochard 2009; Hoffmann et al. 2011; Mitchell et al. 2013; Nardini et al. 2013; Urli et al. 2013). Preliminary experiments indicate that mortality risk appears to increase substantially above 50 % loss conductivity in gymnosperms and closer to 80 % loss in angiosperms (Brodribb and Cochard 2009; Urli et al. 2013) (see also Pratt, this volume).

Hydraulic impairment due to embolism and accumulated damage will likely interact with other mechanisms of mortality, including the interdependent plant carbon status (McDowell et al. 2011), but nonetheless appears to be a prominent explanatory variable in explaining cross-species patterns of drought-induced mortality. Hoffmann et al. (2011) found that the percent loss hydraulic conductivity, explained 55 % of the variation in dieback across 22 angiosperm species in the southeastern United States. Nardini et al. (2013) found that the water potential at which 50 % of hydraulic conductivity is lost (P_{50}) captured 90 % of the variation in mortality rates across six species in Italy. Similarly, integrated wood anatomy traits, especially wood density, are correlated with mortality rates after drought in tropical ecosystems globally as well (Kraft et al. 2010; Phillips et al. 2010). Because many drought-induced mortality events are multiyear and last beyond the inciting drought,

the extent and limits of regrowth of new xylem and repair of embolism are thought to be quite important as well (Anderegg et al. 2012a; Brodribb et al. 2010), perhaps explaining the differential mortality sensitivities between gymnosperms and angiosperms.

A large array of nonhydraulic characteristics will influence vulnerability to drought as well, including coordination of leaf water balance and stomatal regulation (Mitchell et al. 2013), allocation across tissues such as root-to-leaf-area ratios (West et al. 2008), drought characteristics such as intensity and seasonality (Anderegg et al. 2013a), and soil and topoedaphic characteristics such as characteristic moisture curve (Koepke et al. 2010). Rooting depth is another key trait that can determine water availability and mortality during drought (Paddock et al. 2013). Nevertheless, wood anatomy and hydraulic traits present a promising avenue for evaluating, modeling, and predicting the vulnerability of tree species with future climate changes.

4 Plasticity in Wood Anatomy and Hydraulics over Time and Space

Wood anatomy and plant hydraulics are known to vary in time and in space within the same species. Nevertheless, the magnitude of intraspecific variation in contrast to interspecific variation of hydraulics is less well known (e.g., Lamy et al. 2013) (see also Hacke, this volume). A large number of studies have quantified anatomical and physiological differences in wood in species in contrasting environments, especially along moisture gradients (e.g., Alder et al. 1996; Maherali and DeLucia 2000b). A recent meta-analysis synthesized these studies and found that intraspecific variation of a key hydraulic trait (P_{50}) was ecologically relevant, equivalent to 33 % of the variation across species within the same genus and 20 % of the variation within a plant functional type (Fig. 9.6) (Anderegg 2014). Furthermore, intraspecific variation seemed to be higher in angiosperms than in gymnosperms (Anderegg 2014), which fits with understanding of key anatomical differences between the groups (Johnson et al. 2012). Finally, this key trait was poorly captured in plant functional types used to model vegetation response to drought under climate scenarios (Anderegg 2014).

Temporal variation of plant hydraulics is less well known. Tree ring records indicate that many wood anatomical components are sensitive to climate parameters during the years in which they are formed, which suggests that these anatomical differences could affect hydraulics over time (Fonti et al. 2010; Olano et al. 2013). For example, wood density has been shown to increase in oak trees in years following a severe drought (Corcuera et al. 2004) and an analysis of contemporary and paleoclimate effects on vessels in *Quercus macrocarpa* tree rings showed a significant positive relationship between spring temperatures and earlywood vessel diameter and conductivity (Voelker et al. 2012). The number of functional xylem rings will

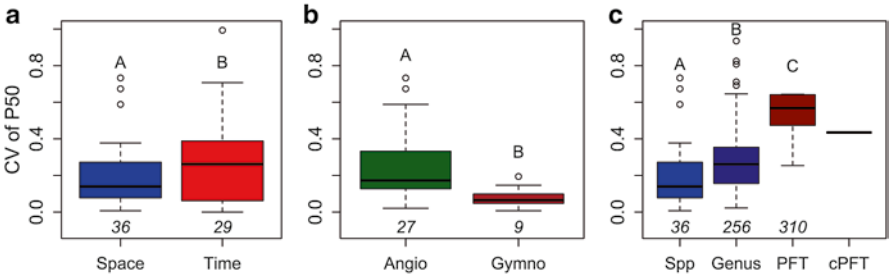

Fig. 9.6 Coefficient of variation of the water potential at which a plant stem reaches percent loss of hydraulic conductivity (P_{50}) across (**a**) space versus time within a given angiosperm species, (**b**) spatially across angiosperms versus gymnosperms within a given species, and (**c**) comparing within-species spatial variation, within-genus variation, within-plant functional type (PFT) variation (tree PFTs only), and across PFT variation (here "cPFT" for cross-PFT). Numbers below bars indicate the sample size of the number of species included. Letters denote statistical significance at $p < 0.05$. Adapted from Anderegg (2014)

also determine the degree of potential plasticity of hydraulic architecture in response to changes in climate. For example, in the oaks described above, the species' water transport relies strongly upon xylem formed in the same year, giving rise to high plasticity in response to climate (Voelker et al. 2012). Anatomical studies have indicated that individual rings differ in their hydraulic properties and vulnerability to embolism (Melcher et al. 2003). And at a whole-plant level, accumulated damage through a mechanism like cavitation fatigue (Hacke et al. 2001b) or acclimation following a severe stress can also likely occur. Nonetheless, the magnitude and ubiquity of these processes is largely unknown.

Spatial and temporal variation in wood anatomy and hydraulic function can arise from two processes—genetic variation or phenotypic plasticity. The balance of these two holds immense importance for the ability of woody species to adapt to shifting climate regimes (Nicotra et al. 2010). If intrapopulation genetic variability is limited and interpopulation variability is large and plasticity is low, leading to local adaptation, then many regions of a species' range would be vulnerable to a change in climate (Franks et al. 2013). On the other hand, if plasticity is high, many individual plants may have scope for adapting to climate shifts in situ, allowing for greater resilience (Nicotra et al. 2010). A compilation of common garden experiments found that local adaptation and clinal variation in genetics and plant traits are quite common in woody plants (Alberto et al. 2013), but the ranges and prevalence of phenotypic plasticity are less well known. Nevertheless, as mentioned above, wood structure and its hydraulic properties can vary dramatically with axial position in tall trees, consistent with substantial plasticity during ontogeny that allows them to cope with increasing xylem tension driven by gravity and cumulative frictional resistances to flow as they increase in height (Fig. 9.3). In Douglas-fir trees ranging in height from 6 to 85 m, P_{50} ranged from about −2 MPa in trunks to −8 MPa in uppermost branches and tracheid pit aperture conductance declined exponentially

with increasing resistance to embolism. Extrapolation of the height-related trend in pit aperture conductance suggested that pit conductance would fall to zero (i.e., zero water transport) at a height of 99–123 m in trunks, consistent with recorded maximum heights for this species (Domec et al. 2008). Thus, in tall tree species, height-related trends in wood anatomy and hydraulics may serve as an adequate proxy for responses to increasing aridity.

5 Future Directions

The emergence of global databases of wood anatomy and plant hydraulic traits, combined with the urgent need to understand and predict woody plant responses to global environmental change, presents a number of exciting and promising research directions. A major challenge revolves around connecting wood anatomy to demographic outcomes and fitness in a changing environment (e.g., Pratt et al. 2014). For example, how meaningful are hydraulic safety margins and are they indicative of true thresholds in vulnerability to drought? Similarly, after what hydraulic thresholds do plants risk mortality and what components and degrees of hydraulic dysfunction can be repaired and survived? Cross-species experiments in glasshouses that can carefully control and monitor water stress and whole-tree fluxes (Urli et al. 2013) and experiments that monitor recovery after a given stress (Ogasa et al. 2013) are greatly needed. To date, we lack a detailed and mechanistic understanding of embolism refilling, and how much it actually occurs in nature, particularly given recent conflicting interpretations of the potential impact of sampling artifacts on the apparent magnitude of daily embolism and refilling in some studies (Wheeler et al. 2013). This uncertainty is a major obstacle to understanding levels of hydraulic risk and lethal thresholds in response to drought and temperature stress.

A second promising research avenue involves the investigation of spatial and temporal variation in wood anatomy and plant hydraulics, and how much of this variation is genetically determined versus phenotypic plasticity (Anderegg 2014). In particular, there are relatively few common garden experiments that have measured anatomical or hydraulic traits (but see Lamy et al. 2013; Schreiber et al. 2011; Wortemann et al. 2011), which are useful in determining the relative influence of adaptation versus plasticity, and also relatively few studies that quantify trait variation of multiple coordinated traits such as gas exchange, morphology, and hydraulic traits across a species range (but see Martínez-Vilalta et al. 2009). Additionally, the temporal scales and potential for turnover and plasticity in anatomy and hydraulic traits over multiple years is not well known. Together, these types of studies can help illuminate how pervasive is local adaptation, when and where in a species' range it could be vulnerable to drought or temperature stress, and how much plasticity can buffer a rapidly changing environment due to climate change.

Ultimately, climate change will have a profound effect on woody plants globally and the ecosystem functions and services they provide. The rates of current and future climate change meet or exceed the fastest rates observed in previous mass

extinction events in the paleoclimate record. Better understanding of the mechanisms through which climate affects plant hydraulics and, in turn, how plant characteristics mediate physiological and demographic responses to a change environment will facilitate prediction of climate change impacts on ecosystems and society.

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