

INVITED REVIEW

A dynamic yet vulnerable pipeline: Integration and coordination of hydraulic traits across whole plants

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Abstract

The vast majority of measurements in the field of plant hydraulics have been on small-diameter branches from woody species. These measurements have provided considerable insight into plant functioning, but our understanding of plant physiology and ecology would benefit from a broader view, because branch hydraulic properties are influenced by many factors. Here, we discuss the influence that other components of the hydraulic network have on branch vulnerability to embolism propagation. We also modelled the impact of changes in the ratio of root-to-leaf areas and soil texture on vulnerability to hydraulic failure along the soil-to-leaf continuum and showed that hydraulic function is better maintained through changes in root vulnerability and root-to-leaf area ratio than in branch vulnerability. Differences among species in the stringency with which they regulate leaf water potential and in reliance on stored water to buffer changes in water potential also affect the need to construct embolism resistant branches. Many approaches, such as measurements on fine roots, small individuals, combining sap flow and psychrometry techniques, and modelling efforts, could vastly improve our understanding of whole-plant hydraulic functioning. A better understanding of how traits are coordinated across the whole plant will improve predictions for plant function under future climate conditions.

KEYWORDS

capacitance, iso/anisohydry, P50, plant hydraulics, soil nutrients, vulnerability to embolism

1 | INTRODUCTION

Knowledge of the hydraulic properties of plants is crucial to our understanding of how they function because of the inescapable link between CO₂ assimilation and evaporative water loss from leaves. This water must be replaced by the vascular network or the leaves will desiccate, air bubbles (embolisms) may propagate throughout the network, and the plant may die. This link is responsible for the strong correlations observed between whole-plant hydraulic conductance and photosynthetic rates (Brodribb, Holbrook, & Gutiérrez, 2002; Hubbard, Ryan, Stiller, & Sperry, 2001; Meinzer et al., 1995) and growth rates (Fan, Zhang, Hao, Ferry Slik, & Cao, 2012; Smith &

Sperry, 2014; Zhang & Cao, 2009). Stomatal responses to water stress are a crucial component of how plants maintain adequate carbon gain yet avoid desiccation during drought. Under well-watered conditions, stomatal conductance (g_s) tends to be high, enabling high photosynthetic rates and plant growth. However, when evaporative demand exceeds the ability of roots to supply water to the transpiration stream, g_s declines to protect the plant hydraulic system from embolism and further desiccation. Furthermore, periods of declining soil moisture are commonly associated with increased evaporative demand (e.g., increased vapour pressure deficit, VPD). Thus, understanding how plants control g_s to minimize water loss during drought while maintaining carbon gain for growth and productivity is critical

to predicting species' responses under current and future water stress. Tight coordination of whole-plant hydraulic conductance and g_s (e.g., Figure 1, which shows this coordination across species) causes increased stomatal opening in sunlit leaves when some leaves on the plant have either been removed (Meinzer & Grantz, 1990; Pataki, Oren, & Phillips, 1998) or shaded (Whitehead et al., 1996). These shifts contribute to the homeostasis of leaf water potential and whole-plant gas exchange: when the number of leaves is reduced or when shading causes volume flow rate through some leaves to decline, g_s increases in the remaining leaves at a given leaf water potential. These shifts also highlight the integrated nature of hydraulics across the whole plant and emphasize the contributions of nonhydraulic and structural components such as the ratio of leaf area to root area, stem cross-sectional area, stomatal control, and contributions of indirectly hydraulic components such as path length, among others.

The field of plant hydraulics is a fairly recent focus within plant eco-physiology and has important distinctions from more traditional plant-water relations, which has a much longer history (Dixon & Joly, 1895; Tyree & Zimmermann, 2002). Namely, although plant-water relations include studies on parameters such as the turgor loss point (TLP) of leaves and stomatal conductance, plant hydraulics is focused on the physiology of water movement from the roots to the leaves and reproductive structures, including its necessity, magnitude, limitations, and relation to other physiological processes. Most of the focus of plant hydraulics is on the apoplastic component of the pathway within the xylem. However, it also includes important segments within the symplast, specifically through the root endodermis, within leaves, and also the contributions of living and nonliving cells to water storage and its release to the xylem (i.e., capacitance). In terms of distances involved, the paths through living tissues of roots and leaves are often

trivial components of the soil-leaf pathway. These distances must be short to maintain the flow rates plants exhibit, because the hydraulic resistances are extraordinarily high relative to the superhighway of the xylem conduit network. In roots, the radial hydraulic conductivity from the soil into the vasculature of absorbing roots is estimated to be $\sim 2 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-1}\cdot\text{MPa}^{-1}$ (Steudle & Peterson, 1998), which is more than 10 orders of magnitude lower than typical saturated xylem conductivities. This extremely low radial conductivity does not limit the conductance of the root system, and thus the entire plant, only because of its very short length and the extremely large surface area of the fine roots that are connected in parallel. In leaves, the total (xylary and extraxylary) resistance can represent 50–90% of the total plant resistance, and the resistance of each of the two components is estimated to be roughly equivalent (Sack & Holbrook, 2006).

The majority of the research in plant hydraulics has focused on measurements of small-diameter (~ 1 cm) woody branches and roots that permit the use of the entire xylem cross section. The reasons for this are simple: Many of the techniques employed by researchers to assess traits such as hydraulic conductivity and vulnerability to embolism are most easily made on these narrow and woody segments. These are also the tissues that are most easily collected, and their removal often causes minimal impact on plant function, thus allowing concomitant measurements of other physiological parameters. This research has been extremely informative. Studies on xylem structure and function in branches have linked various vascular system traits to species distributions (e.g., Brodribb & Hill, 1999; Oliveira et al., 2019; Pockman & Sperry, 2000; Trueba et al., 2017), the ability of plant communities to tolerate or adjust to shifts in water availability (Anderegg et al., 2018; Rosas et al., 2019), and vulnerability to mortality (Adams et al., 2017; Choat et al., 2012), among others. Although historically the plant hydraulics field has concentrated largely on woody tissues, the last decade has seen an explosion of work on leaves (e.g., Blackman et al., 2018; Brodribb & Feild, 2010; Nardini, Pedá, & Salleo, 2012; Sack & Holbrook, 2006) and an uptick in studies on herbaceous species (e.g., Ocheltree, Nippert, & Prasad, 2012; Cardoso, Brodribb, Lucani, DaMatta, & McAdam, 2018; Dória, Podadera, et al., 2018; Johnson, Jordan, & Brodribb, 2018). Many of the techniques developed for leaves are applicable to herbaceous species and the future will likely include further expansion into this area.

One of the most common measurements made in studies on plant hydraulics is testing the vulnerability of water transport to desiccation-induced hydraulic failure. Vulnerability curves depict the organ- and species-specific loss of hydraulic conductance with decreasing xylem pressure, which can be caused by embolism propagation throughout the network of conduits and/or increases in extraxylary hydraulic resistance (in leaves, for example, Trifiló, Raimondo, Savi, Lo Gullo, & Nardini, 2016; Scoffoni et al., 2017). These curves are often characterized by the P50, which is the pressure at which 50% of the hydraulic conductance has been lost. The P50 of leaves and stem segments has been determined for hundreds of species across the globe. Perhaps the most visually striking comparison of this metric across habitats was made by Maherali, Pockman, and Jackson (2004) and has been updated here (Figure 2). The most

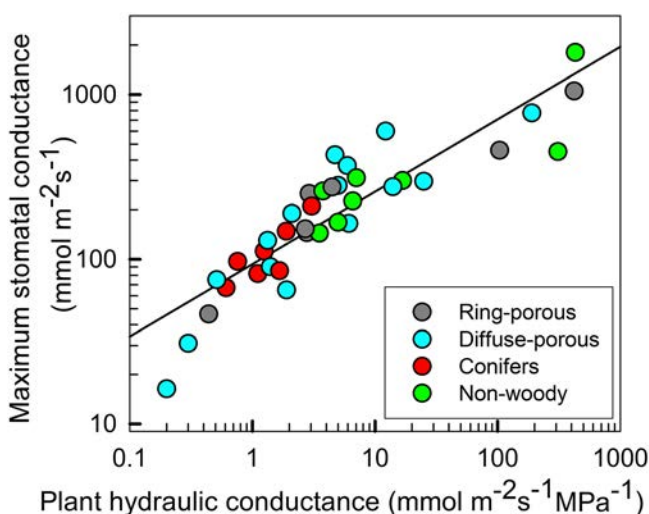


FIGURE 1 Relationship ($r^2 = .83$, $P < .001$) within plant groups between maximum stomatal conductance (g_s) and whole-plant hydraulic conductance (K_{plant}). Data plotted in log-log form for individual species within the four broad classes of plant anatomical groups. Data and sources are shown in Table S1

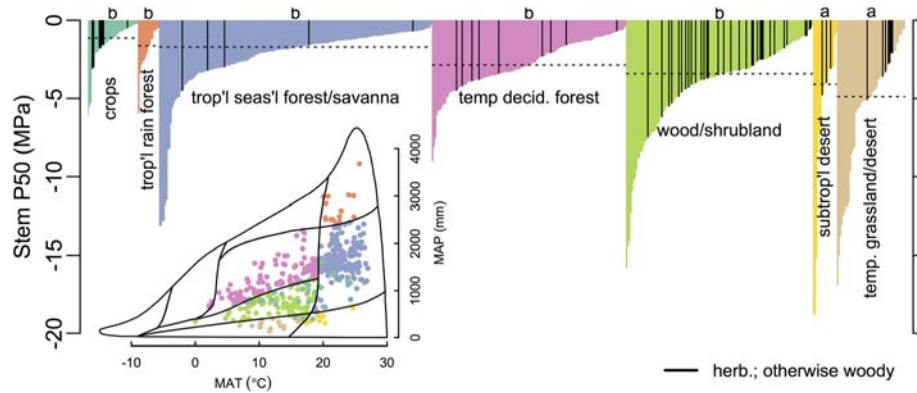


FIGURE 2 The distribution of 582 stem P50 values from 536 species categorized by broad ecological group (inset; also see notes in Table S1 for how groups were assigned). Groups are ordered left to right by decreasing median P50 (dashed lines). 89% of values came from woody species (colors), whereas the remainder were herbaceous (black). Levene's test indicated variance differed across groups ($P < .0001$). Letters indicate significant differences in variance between groups as determined by Tukey's honestly significance difference performed on an analysis of variance of residuals from group medians. Crops showed the least variance, whereas subtropical desert showed the most. Inset: Whittaker plot of median mean annual precipitation (MAP) and mean annual temperature (MAT) for each species. Data, sources, and analysis details are listed in Table S2 [Colour figure can be viewed at wileyonlinelibrary.com]

conspicuous part of this figure is not the change in P50 values among the biomes, but the variability of the metric within them. The mean value within a biome does become more negative as aridity increases, but the variation within a community type is noteworthy, because it implies that a broad range of overall hydraulic strategies can contribute to evolutionary success in a given environment. Indeed, as mean annual precipitation declines (Figure 2, inset), the variation in branch P50 values within a biome increases. Furthermore, given the integrated nature of plant hydraulics, this variation suggests coordination and trade-offs among a series of traits along the entire water transport pathway. Thus, the primary question of this review is the following: What are these coordinated traits and the trade-offs among them that lead to this large variation among P50 values within a community? The answer fundamentally is related to properties of the other parts of the plant that are not being characterized by this single metric.

Our focus in this review is on the coordination and integration of hydraulic traits that lead to the wide variation in leaf, stem, and root P50 values within communities (Figures 3 and S1). However, other species characteristics also contribute to the variability. For example, differences in life history strategies, such as dormancy (Nardini & Tyree, 1999) or leaf shedding (e.g., Bullock & Solis-Magallanes, 1990), would limit the need for particularly negative P50 values in an arid environment. Furthermore, in woody plants, mechanical requirements to tolerate forces such as gravity and wind may demand higher wood density that is achieved by having thicker conduit walls (Lachenbruch & McCulloh, 2014). Denser wood is also required to balance the greater negative pressure within the xylem conduits of plants growing in drier habitats (Hacke, Sperry, Pockman, Davis, & McCulloh, 2001) and thus correlates with more negative P50 values (Hacke et al., 2001; Jacobsen, Ewers, Pratt, Paddock, & Davis, 2005). Thus, for a given amount of carbohydrate produced, plants making denser xylem, which tends to be more resistant to embolism, should also have slower growth rates (King, Davies, Nur Supardi, & Tan, 2005; Poorter et al., 2008). There may also be fundamental differences between species

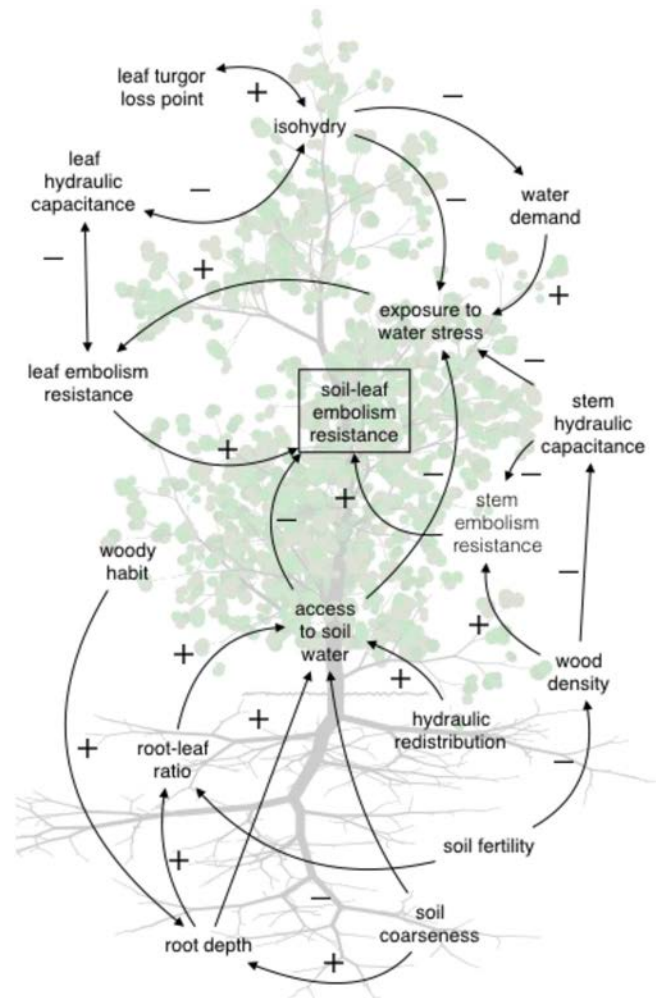


FIGURE 3 The factors influencing soil-leaf embolism resistance in plants. Single-ended arrows indicate causation, whereas double-ended arrows indicate correlation. Plus and minus symbols show positive and negative relationships, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

with different growth habits. For example, lianas may have fewer mechanical demands than trees, which may result in them being less overbuilt in terms of P50 than trees (De Guzman, Santiago, Schnitzer, & Álvarez-Cansino, 2017; Johnson, Domec, Woodruff, McCulloh, & Meinzer, 2013). Alternatively, many shrubs have multistemmed “trunks,” which can act to isolate embolisms independent of conduit structure, which reduces the need for extremely negative P50s (i.e., a multistemmed shrub may have a less negative P50 than a co-occurring single-stemmed plant; Schenk et al., 2008).

For much of our discussion, we assume that the branch P50 values correlate roughly with the daily minimum leaf and branch water potentials (P_{min}). Meaning, we assume that species having a more negative P50 also experience more negative water potentials, that is, a fairly constant hydraulic safety margin (P_{min} -P50). This assumption may not be accurate, particularly when comparing species with contrasting stomatal behaviours under water-limited conditions or when comparing branches in angiosperms and conifers, because conifer branches tend to have larger safety margins than angiosperms (Choat et al., 2012; Meinzer, Johnson, Lachenbruch, McCulloh, & Woodruff, 2009). However, within a wood type (e.g., diffuse-porous), the safety margins of branches do not differ across habitats in conifers and are nearly constant among angiosperms (Choat et al., 2012). The exception among angiosperms were plants from Mediterranean and woodland habitats (i.e., the driest habitats considered), which tended to have higher safety margins than the plants from other habitats in the analysis by Choat et al. (2012).

Our review is not intended to cover all aspects of the soil–plant–atmosphere continuum but instead to focus on how often unmeasured variables contribute to a commonly measured metric (e.g., branch P50). Other recent reviews have examined how mathematical models have depicted plant hydraulic fluxes (Mencuccini, Manzoni, & Christoffersen, 2019) and the impact of plant hydraulics on the terrestrial water cycle (Fatichi, Pappas, & Ivanov, 2016). Both of these reviews have explored these topics from the scale of tissues or individuals to the globe, whereas our focus is mainly on fluxes from the soil to the individual or within the individual. Specifically, here, we examine how differences in rhizosphere traits, stomatal regulation of leaf water potential, hydraulic capacitance, and coordination of traits between leaves and branches affect the plant's risk of hydraulic failure. We then discuss potential experimental and modelling approaches to furthering our understanding of whole-plant hydraulic function.

Although we largely treat the traits discussed in the sections below separately, there is clearly coordination among them (Figure 3; Reich, 2014; Pivovarovoff, Cook, & Santiago, 2018; Fu & Meinzer, 2019). For example, many species that are highly resistant to embolism share many of the following characteristics: higher wood density, shallower roots, lower root-to-leaf area ratio, more negative leaf water potentials at turgor loss, less sensitive stomatal regulation of leaf water potential (i.e., more anisohydric species), lower daily reliance on discharge and recharge of stored water (i.e., capacitance), and so forth. However, except for possibly the relationship between stem capacitance and P50 because of its correlation

with wood density (see below), the coordination of the other traits is not necessarily causative. For example, a tree growing near a stream could have poor stomatal regulation of water potential and have vulnerable xylem, because consistently high xylem pressures would not require strong stomatal regulation to maintain an adequate hydraulic safety margin.

2 | DIFFERENCES IN ROOTING DEPTH, SOIL TYPE, AND SOIL NUTRITION

Species that have roots with access to a reliable water supply tend to have branches with more vulnerable xylem than co-occurring species with roots that do not access the reliable water source. Often, the roots of the more embolism resistant species are more shallowly distributed than those of the more vulnerable species (e.g., Hacke, Sperry, & Pittermann, 2000; Jackson, Sperry, & Dawson, 2000; Johnson, Jordan, & Brodribb, 2018; Lopez, Kursar, Cochard, & Tyree, 2005). Although these patterns conform to our understanding of the relative predictability of water sources in shallow versus deeper soils, various parameters can complicate the patterns. For example, hydraulic redistribution (HR) from neighbouring deeply rooted plants can result in shallowly rooted species experiencing milder water potentials and forming more vulnerable wood than the same species at sites without HR (Jackson et al., 2000). Domec, Warren, Meinzer, Brooks, and Coulombe (2004) found that at sites with deep roots that partially replaced water taken up from shallow soil layers, Douglas-fir and ponderosa pine trees maintained greater root hydraulic function relative to trees at sites with little HR during the dry season. Although branch vulnerability curves were not measured in this study, the pre-dawn and midday leaf water potential values were less negative at the sites that benefited from HR than those that did not, suggesting that the branches may exhibit differences in xylem vulnerability to accommodate the water stress.

We used a model to explore how the hydraulic properties of different components in the soil to leaf pathway contribute to the overall vulnerability of the pathway. Models that predict soil–plant–water relations and their responses to the temporal shifts in abiotic variables must combine soil–root hydrodynamics with branch- and leaf-level physiological constraints. However, there are a plethora of complications when modelling plant–water relations, including soil properties and differences in root, stem, branch, and leaf hydraulic parameters within and across plants. In our approach, the water movement along the xylary pathways was modelled by including fine-scale spatial processes representing nonlinearities in hydraulic properties (vulnerability curves and soil–root contact). Hence, within each of the soil–plant compartments, the goal was to retain sufficient representation of key hydrodynamic and physiological processes while allowing for integration to the plant level (Huang et al., 2017). To assess the relative importance of soil-to-root versus root-to-leaf conductance in whole-plant (i.e., soil–leaf continuum) hydraulic conductance, we modelled the decline in whole-plant conductance and its components as water stress increased under two different scenarios (see Supporting

Information for details; Figure 4a–d). To evaluate the induced changes along the entire soil–leaf continuum, the various hydraulic conductance functions were integrated over the entire flow path. Specifically, we compared changes in the root-to-leaf area and soil texture (Figure 4e–h). A soil's texture influences its water-holding capacity, water-release properties, and the decline in soil-to-root conductance that can result in species with the same rooting depths experiencing different branch and leaf water potentials in different soils (Sperry, Adler, Campbell, & Comstock, 1998). Specifically, coarser-textured soils bind water less tightly and therefore tend to have lower water content at a given matric potential than loamier soils. Perhaps counter-intuitively, though, plants growing on sandier soils tend to maintain milder water potential values and often exhibit more vulnerable xylem than those on loamier soils (Barnard et al., 2011; Domec et al., 2015; Hacke et al., 2000; Sperry & Hacke, 2002). Water uptake in sandy soils is usually limited to high soil water potentials because of the sharp decline in soil-to-root conductance with matric potential. This constraint is the reason why many perennial species in biomes that are both arid and have sandy soils maintain a portion of the root system in very deep soil that has consistently high water potential (Domec et al., 2012; Ewers, Oren, & Sperry, 2000; Sperry et al., 1998), which also increases the root-to-leaf area ratio.

Our modelling comparisons indicate declines in hydraulic conductance within organs and the whole plant as soils dry (Figure 4a–d). These results also reflect the greater influence of the root vulnerability curve on the whole-plant curve as the root-to-leaf area ratio is increased (i.e., compare proximity of root vulnerability curve with the whole-plant curve when the ratio is increased from 1.5 to 9). Importantly, these results emphasize that a given branch and leaf vulnerability can be associated with different whole-plant vulnerability because of the influence of and the tight coordination with other traits. Furthermore, the results show the effect of soil texture on soil-to-leaf hydraulic conductance and the greater influence of root-to-leaf area ratio on whole-plant hydraulic conductance than vulnerability to embolism of any single organ (Figure 4e–h). These data support observations and previous modelling efforts that on sandy soils plants maintain higher hydraulic conductance by exhibiting a higher root-to-leaf area ratio rather than by having a more negative root P50, because the higher root-to-leaf area ratio minimizes the development of limiting hydraulic resistances in the soil–root continuum (Sperry et al., 1998). Furthermore, there is no advantage in having more embolism resistant plant organs in environments where soil hydraulic conductance limits water transport (Figure 4, but also see Ewers et al., 2000; Sperry et al., 1998; Johnson, Berry, et al., 2018). Indeed, reducing root-to-leaf area may actually increase the probability of hydraulic failure as soils dry (Teskey, Hinckley, & Grier, 1983), even if plants produce more embolism-resistant xylem (Figure 4; Ewers et al., 2000). It is worth noting that this result assumes that the roots stay hydraulically connected to the soil, which may not always be the case (Cuneo, Knipfer, Brodersen, & McElrone, 2016; North & Nobel, 1991). Lower root-to-leaf area reduces the potential for water uptake during drought, which causes significant embolism, regardless of embolism resistance, and a loss of whole-plant hydraulic conductance (Domec

et al., 2015; Sperry & Love, 2015). Inversely, for plants of a given architecture growing on soil with fine texture (loam to clay), greater embolism resistance is the only way to limit soil–leaf loss of conductance as soil dries (Figure 4e–h). This would allow the plant to withdraw more water held at low soil matric potential and thus maintain significant water extraction capacity. As soil texture becomes coarser, the difference between the vulnerability curves for the soil-to-leaf and root-to-leaf pathways increases, because of the decline in soil-to-root hydraulic conductance (Figure 4e–h). The model predicts that this difference is minimized by high root vulnerability to embolism and high root-to-leaf area (Figure 4h).

Consistent with these modelling results, Domec et al. (2015) found that the branch P50 of the angiosperm species examined became more negative on loamier soil, although P50 of the conifer (*Pinus taeda*) did not differ between the two sites. Interestingly, Hacke et al. (2000) did observe a more negative P50 in branches of *P. taeda* trees growing on loamy soils compared with those on sandy soils, but the differences in soil type were much more pronounced in their study than in Domec et al. (2015). Similarly, Sperry and Hacke (2002) found that root xylem of eight shrub species from the Utah Great Basin was almost 1 MPa more resistant to embolism at a loamy site versus a sandy site. While the model indicates why species in sandy systems may favour higher root-to-leaf area ratio over greater resistance to embolism, there are many examples of species using this strategy co-occurring with species that are more shallowly rooted and exhibit extremely negative P50 values (Hacke et al., 2000; Johnson, Domec, et al., 2018). In some cases, the plants with less negative P50s die during droughts (Hacke et al., 2000; Johnson, Domec, et al., 2018), as predicted by the model, but in other cases, the reverse is true (McDowell et al., 2008). Determining the circumstances under which each of these types of plants dies would be useful for landscape-level models of plant communities under future climate scenarios.

Environmental changes that increase the availability of resources (either above or below ground) result in the long-term acclimation of a less conductive (per unit leaf area) hydraulic system because of anatomical acclimation (Mencuccini, 2003). In particular, greater soil fertility can increase the risk of embolism through less negative P50 values (Oliveira et al., 2019; Pivovarov, Santiago, Vourlitis, Grantz, & Allen, 2016; Zhang et al., 2018) and by affecting the partitioning between root and leaf area by increasing shoot growth at the expense of root growth (McCarthy, Oren, Finzi, & Johnsen, 2006). This transpiring versus absorbing water disequilibrium imposes a rapid loss of whole-plant hydraulic conductance as soil dries (Bucci et al., 2006; Zhang et al., 2018), thus leading to hydraulic failure and plant mortality (Linder, Benson, Myers, & Raison, 1987; Villar-Salvador, Peñuelas, & Jacobs, 2013). Similar to the morphological changes driven by soil texture, plants lower their root-to-leaf area following fertilization, which reduces their water uptake capability and causes the soil-to-root conductance to be the main determinant of the soil-to-leaf conductance hydraulic continuum (Figure 4e–h; Ewers et al., 2000).

These changes in plant architecture due to differences in nutrient levels can drive shifts in organ P50 values. After long-term N and P additions, P50 declined consistently across five tree species growing

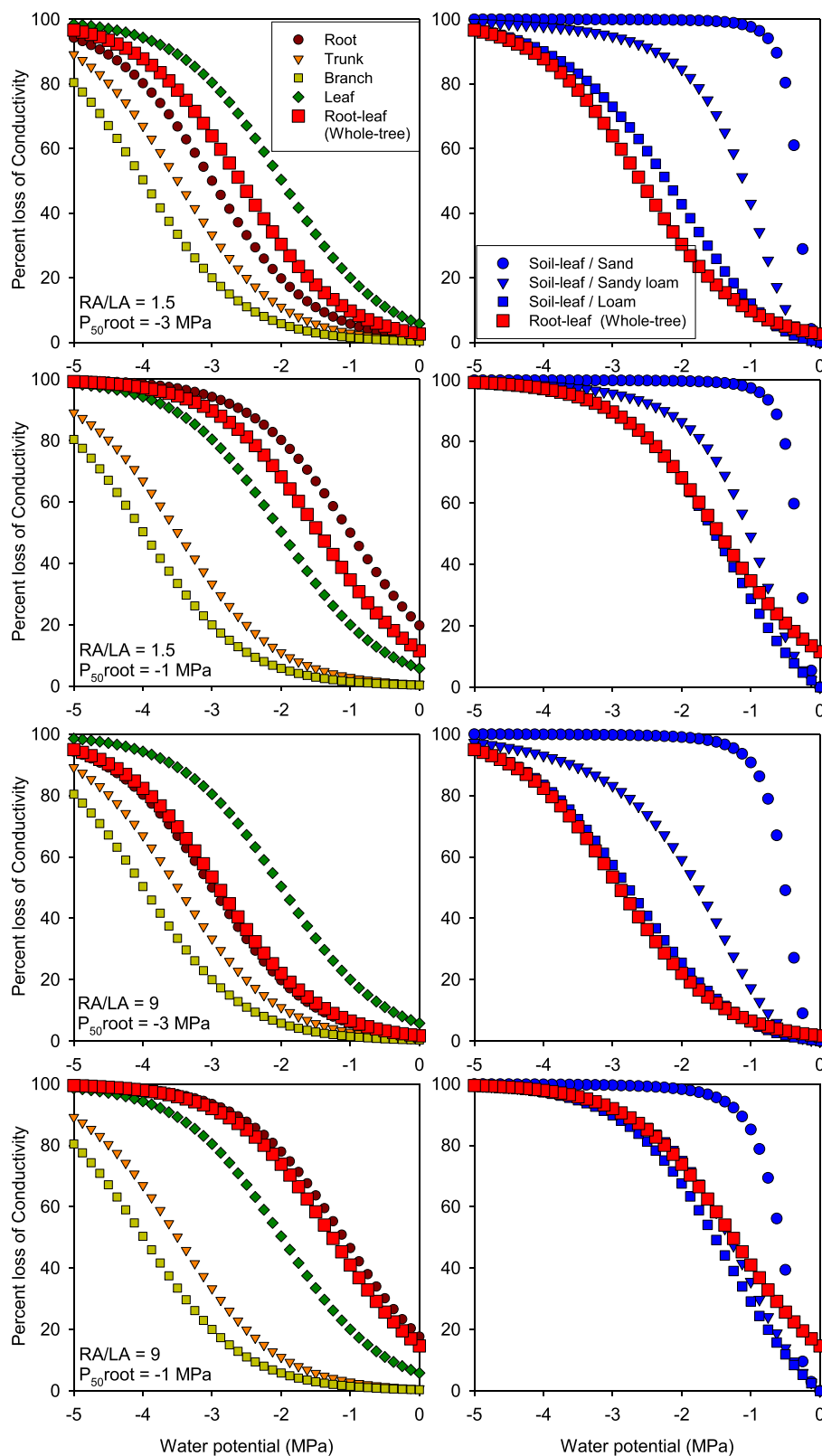


FIGURE 4 (a–d) Vulnerability to embolism in individual organs and calculated root to leaf (whole-tree) hydraulic vulnerability curves for two different values of root to leaf area ratio (RA/LA) and two values of root water potentials at which 50% of hydraulic conductivity occurred (P_{50}). (e–f) Simulated soil to leaf loss of hydraulic conductance under three contrasting soil types. For comparison, whole-tree losses of hydraulic conductances from Panels a–d are also given (in red) [Colour figure can be viewed at wileyonlinelibrary.com]

in the savannah of central Brazil (Bucci et al., 2006), which is the opposite pattern observed when N was added to poplar trees (Hacke et al., 2010) and across a naturally occurring gradient in P content in tropical Brazil (Oliveira et al., 2019). At the Duke Free-Air CO₂ Enrichment site, even though leaves of N-fertilized trees showed lower hydraulic conductance, no effect on P50 was discernible (Domec et al., 2015). The differences among the findings of these studies likely have to do with coordinated changes in other traits. For example, Bucci et al. (2006) found that the more negative P50 values were associated with increased leaf area per plant and more negative daily minimum leaf water potential, whereas Hacke et al. (2010) found milder P50 values were associated with lower wood density, thus highlighting the value of measuring a range of traits across the plant. Alternatively, if the plant does not make allometric changes in response to greater N availability, the N content of leaves would rise, which could increase the photosynthetic rate and result in either greater water use efficiency or an increase in stomatal conductance (Wright, Reich, & Westoby, 2003), which would decrease leaf water potential.

A final way in which the rhizosphere can influence the leaf and branch water potentials is by roots acting as hydraulic bottlenecks. Although recent evidence suggests it may not always be the case (Rodriguez-Dominguez, Carins Murphy, Lucani, & Brodribb, 2018; Skelton, Brodribb, & Choat, 2017), roots are often more sensitive to embolism than stems and can greatly influence soil-leaf hydraulic conductance in the same way as an increased rhizosphere limitation (Figure 4). Essentially, by having roots that embolize, the whole-plant hydraulic resistance increases steeply and the water supply to the leaves drops. In response to this sudden decline, stomata close, thus limiting a further decrease in water potentials, leaves and stems could experience and the need for more embolism resistant xylem. This phenomenon has been observed in species in a Brazilian savanna system (Domec et al., 2006), the Pacific Northwest of the United States (Domec et al., 2004), an Australian species adapted to riparian areas (Creek, Blackman, Brodribb, Choat, & Tissue, 2018), and modelled in species from the Piedmont of North Carolina (Domec, Schäfer, Oren, Kim, & McCarthy, 2010). Given the diversity of these habitat types, this phenomenon may have been selected for in other plants that have not yet been examined. In addition to loss of axial hydraulic conductance, roots may lose the ability to efficiently transport water radially during periods of water stress (Cuneo et al., 2016).

The effect of rooting depth and/or soil texture on the P50 of leaves remains unknown. Do patterns across branch and leaf P50 remain the same across changes in the rhizosphere, or not? Furthermore, what are the effects of soil texture and nutrition on herbaceous species' hydraulic properties? Rooting depth tends to not be as plastic in herbaceous species as it can be in woody plants (Schenk & Jackson, 2005), which could limit the range of root-to-leaf areas available to herbaceous plants. However, even within shallower soil depths, herbaceous species can have extremely dense root systems, which can supply considerable leaf area and may aid in using water before it reaches more deeply rooted competitors (Nippert & Holdo, 2015).

3 | DIFFERENCES IN STOMATAL CONTROL

The water potentials of the terminal portion of the water transport pathway are influenced by the coordinated traits along the pathway, such as leaf TLP, hydraulic capacitance, leaf specific conductance, soil properties, and moisture availability, but also by the actions of stomata. To the extent that stomata control water potentials, plant species exist along a continuum of stomatal regulation of leaf water potential (Fu & Meinzer, 2019; Martinez-Vilalta, Poyatos, Aguad, Retana, & Mencuccini, 2014; Tardieu & Simonneau, 1998). At one end of the spectrum are isohydric plants whose stomata tightly constrain reductions in leaf water potential during periods of declining soil moisture and/or high VPD. Alternatively, more anisohydric species exhibit much more relaxed stomatal regulation of leaf water potential and, as a result, experience much more negative water potentials during periods of low soil moisture. As one would predict, more anisohydric species tend to have branches (Fu & Meinzer, 2019; Linton, Sperry, & Williams, 1998; Martinez-Vilalta et al., 2014; Pivovarov et al., 2018; Skelton, West, & Dawson, 2015; Vogt, 2001) and leaves (Johnson, Berry, et al., 2018) that are more resistant to embolism propagation. The mechanistic coordination of stomatal behavior and P50 may be through the production of and response to ABA (Brodribb, McAdam, Jordan, & Martins, 2014). Clearly, there are suites of traits that must accompany these differences in stomatal regulation of leaf water potential, such as differences in rooting depth and reliance on stored water.

One of the traits that appears to be most closely associated with a species' relative degree of isohydry is its TLP. Indeed, Meinzer et al. (2016) proposed using the TLP, which can be fairly easily measured, as a proxy for the degree of isohydry, a thorough assessment of which requires much more extensive measurements of gas exchange and water potential under increasingly severe water deficits. Using TLP as a proxy has since been supported by a broad range of species (Fu & Meinzer, 2019; Li et al., 2019). Leaf TLP appears to integrate many upstream parameters within plants. In a comprehensive study examining relationships among TLP and a variety of hydraulic parameters in woody plants, Bartlett, Klein, Jansen, Choat, and Sack (2016) found strong relationships between TLP and leaf and branch P50. Interestingly, they found a common relationship between TLP and leaf P50 among conifers and angiosperms, but separate relationships for the two groups when TLP was compared with branch P50. Among the branches, the conifers exhibited a steeper positive relationship, indicating that for a given decrease in TLP, the branch P50 of conifers becomes much more negative than in angiosperms. Among herbaceous species, TLP also correlates positively with leaf P50 values (Griffin-Nolan et al., 2019). Johnson, Berry, et al. (2018) also found that more anisohydric species were able to adjust their TLP more over the course of a season as soils dried than more isohydric species did. These shifts in TLP were also associated with decreases in the leaf P50 values. Similarly, Cardoso et al. (2018) showed that when sunflowers were exposed to water stress, they reduced their TLP and leaf P50 in concert. This reduction in leaf P50 occurred through structural changes in the midrib xylem.

A more static limitation on water loss than g_s is the cuticular conductance of leaves. The cuticle acts as the last line of defence against water loss during a drought. However, in a study on 17 woody species, Pivovarov et al. (2018) found no relationship between cuticular conductance and a wide range of traits, such as P50, TLP, and degree of iso/anisohydry. Although cuticular conductance was not adjusted in these woody species (Pivovarov et al., 2018), it has been shown to change in response to drought in some herbaceous species (Kosma & Jenks, 2007). Furthermore, it remains unclear the extent to which cuticular transpiration differed among the 17 woody species in the Pivovarov et al. (2018) study. Cernusak et al. (2018) reported greater declines in the relative humidity of intercellular airspaces as VPD increased in a more isohydric species (*Pinus edulis*) than in a more anisohydric one (*Juniperus monosperma*). They argued that differences in the coordination between stem and leaf water potentials between the two species led to structural differences in leaf cell walls (Vesala et al., 2017), which reduced the hydraulic conductivity more in the more isohydric species. If this pattern of lower intercellular relative humidity in more isohydric species is broadly true, it would result in a smaller vapour pressure difference between the inside of the leaf and the atmosphere. For a given cuticular conductance and air vapour pressure, the cuticular transpiration of more isohydric species could be lower. This provocative idea remains a potential area for further research.

4 | DIFFERENCES IN RELIANCE ON STORED WATER

Hydraulic capacitance, the ability of plant tissues to store water and release it to the transpiration stream, can transiently buffer changes in downstream water potential after an increase in the transpiration rate (Figure 5). This transient buffering effect of capacitance on xylem pressure can be quantified using a time constant (τ), which is the product of capacitance and the sum of the radial hydraulic resistance from the storage source to the transpiration stream and the resistance of the axial hydraulic pathway (Phillips, Nagchaudhuri, Oren, & Katul, 1997; Ward, Bell, Clark, & Oren, 2012). This τ value corresponds to the time required for the water potential to reach 63% of its final, steady-state value after an increase in transpiration driven by a step increase in VPD (Figure 5). Thus, species with higher capacitance (for a given hydraulic resistance) have a longer period to react physiologically to an increase in VPD (Martins, McAdam, Deans, Damatta, & Brodribb, 2016; Roddy, Simonin, McCulloh, Brodersen, & Dawson, 2018) and could respond by reducing stomatal conductance or changing the ionic concentration of the sap to locally increase hydraulic conductance (Nardini, Salleo, & Jansen, 2011; Zwieniecki, Melcher, & Holbrook, 2001).

Capacitance in stems is determined from the slope of water release curves (volumetric water lost vs. water potential; $\text{kg}\cdot\text{m}^{-3}\cdot\text{MPa}^{-1}$). In leaves, capacitance values can be determined from pressure–volume analyses (Tyree & Hammel, 1972) and are often expressed on a molar basis instead of mass of water lost (i.e., $\text{mmol}\cdot\text{m}^{-2}\cdot\text{MPa}^{-1}$) to make the units consistent with gas exchanges values. The release of water from

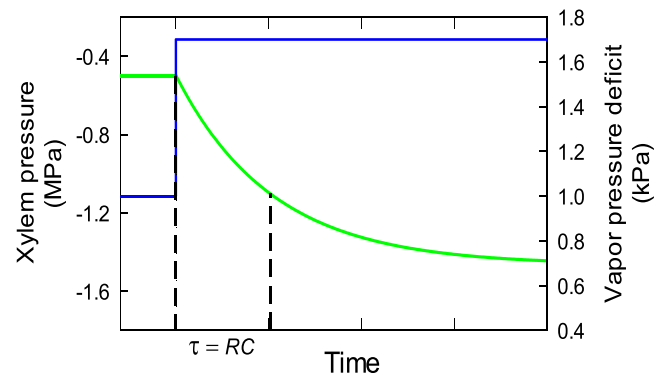


FIGURE 5 Hypothetical time course showing the buffering effect of capacitance on the rate of decline in water potential (green line) following an increase in transpiration induced by a step increase in leaf-to-air vapour pressure deficit (blue line). The time constant (τ = hydraulic resistance * hydraulic capacitance) is the time (between dashed lines) at which xylem pressure has reached 63% of its steady-state value after a step change in transpiration. The simulation assumes no change in stomatal conductance, capacitance, or hydraulic resistance over the time span. In a hypothetical plant devoid of capacitance, the water potential would immediately fall to its final value [Colour figure can be viewed at wileyonlinelibrary.com]

the stems versus leaf tissues of plants exhibits different patterns. In stems, as water potentials become more negative, there is an initial steep, nearly linear portion of the water release curve (McCulloh, Johnson, Meinzer, & Woodruff, 2014; Meinzer, James, Goldstein, & Woodruff, 2003). Most studies have focused on this region of the curve because it has the greatest amount of water released per MPa and also because it corresponds to the range in water potentials experienced by the plants under field conditions of low to moderate water stress. Additionally, injections of deuterated water (D_2O) into the base of the trunk of mature angiosperm and coniferous trees have shown that the velocity and residence time of this tracer are strongly correlated with sapwood capacitance estimated from the initial steep portion of the sapwood water release curve (Meinzer et al., 2003, 2006).

A useful metric for analyzing hydraulic capacitance is the point of diminishing returns (PDR) where the initial steep slope begins to flatten. At pressures more negative than the initial steep portion of the curve, beyond the PDR, the wood contains far less water to release to the transpiration stream. However, recent studies have highlighted the importance of this second stage of capacitive release (Jupa, Plavcová, Gloser, & Jansen, 2016; Richards, Wright, Lenz, & Zanne, 2014), and this portion of the curve may be more closely associated with water potentials experienced in natural settings for some species, especially those that experience more severe water potentials (Fu et al., 2019). In leaves, there are also two distinct linear regions of the water release relationships and they are thought to reflect differences in the water potential component regulating the release. The initial, slow phase is being regulated by both the osmotic and turgor pressure potentials, whereas the faster second phase is predominantly influenced by the osmotic potential (Tyree & Hammel, 1972).

Unlike the other hydraulic traits discussed in this review, the link between woody tissue P50 and capacitance appears to be more causative than correlative. The cost of producing plant organs that are more resistant to embolism has been mechanistically linked to wood density and cell wall thickness. Mechanistically, this need for greater conduit wall thickness (Hacke et al., 2001) and/or thick-walled fibers (Jacobsen et al., 2005) precludes species that experience very negative water potentials from having high capacitance, because of the lack of space to store water. This space limitation is true regardless of where the water is stored (i.e., in parenchyma or the apoplast), assuming a given stem volume. Indeed, this mechanistic link results in a strong positive relationship between P50 and capacitance (McCulloh et al., 2014; Meinzer et al., 2008; Meinzer, McCulloh, Lachenbruch, Woodruff, & Johnson, 2010; Scholz, Phillips, Bucci, Meinzer, & Goldstein, 2011), meaning that as the P50 values become less negative, the capacitance increases. In addition to the mechanistic link between P50 and capacitance, for many species, there also appears to be a functional link between branch capacitance and the daily minimum branch water potential determined by stomatal regulation of transpiration. For nearly all species examined, this coordination results in the daily minimum branch water potential corresponding directly with the PDR (Figure 6). As branch water potentials approach the PDR, the transient buffering effects of capacitance are diminished and any increase in transpiration would be accompanied with a rapid change in water potential of the branch and subtending leaves. For example, if VPD increases rapidly (perhaps a cloud that had been covering the sun moves on), without the transient buffering of stored water, the change in water potential would be propagated through the system very rapidly (Figure 5), which would require structural tolerance of

very negative pressures. Whether stomata of the species on the 1:1 line in Figure 6 are responding to a specific water potential or the rapid change in water potential is unknown. Importantly, though, not all species align to the 1:1 relationship. Specifically, species from a low nutrient site in Australia experienced midday water potential values that exceeded their PDR. One potential explanation for the deviation observed in these species is that the low nutrient concentration in the soil forced species to transpire more in order to acquire the nutrients they require.

One of the benefits of high capacitance is that plants should be able to adjust their stomatal conductance in response to an increase in evaporative demand before water potentials reach dangerously low values. Species with lower capacitance should theoretically have more rapidly reacting stomata, xylem that can tolerate lower water potentials (i.e., low P50), or both. Indeed, high leaf capacitance has been shown to correlate with slower VPD-induced stomatal closure (Fu et al., 2019; Martins et al., 2016). Consistent with this, Fu et al. (2019) found greater leaf capacitance in more anisohydric species than in more isohydric species. This pattern may seem contradictory, because species with higher stem capacitance tend to be more isohydric, but recent evidence suggests that leaf and stem capacitance may be inversely related, meaning species with high leaf capacitance tend to have lower stem capacitance (Fu et al., 2019). At the stem level, species with high stem capacitance tend to have more negative $\delta^{13}\text{C}$ values in their leaves, which indicates they maintain lower relative stomatal limitation of photosynthesis than species with lower stem capacitance (Figure 7). This relationship may be mediated by the trend for species with high stem capacitance to also have high stem hydraulic conductance (McCulloh et al., 2012; Meinzer et al., 2003). The inverse relationship between leaf and stem capacitance may also be related to those organs' hydraulic conductance, which tend to be positively correlated (Sack, Cowan, Jaikumar, & Holbrook,

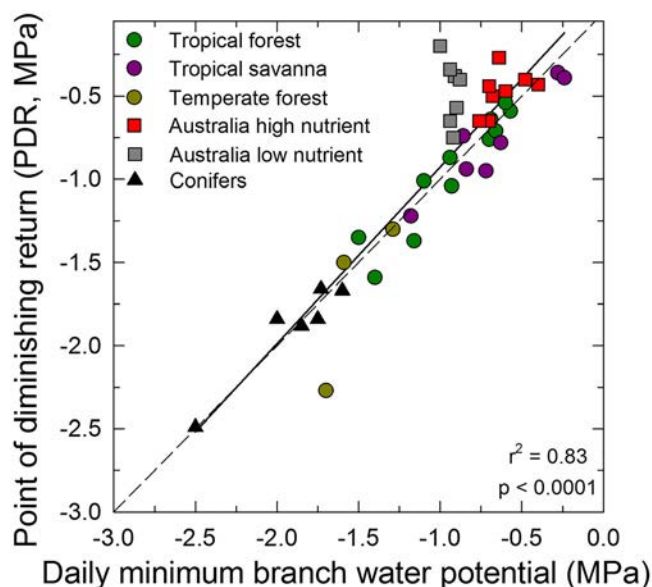


FIGURE 6 The daily minimum branch water potential versus the point of diminishing results on the branch sapwood moisture release curve for 42 woody species from different biomes. Dashed line represents the 1:1 relationship. Data and sources are shown in Table S3 [Colour figure can be viewed at wileyonlinelibrary.com]

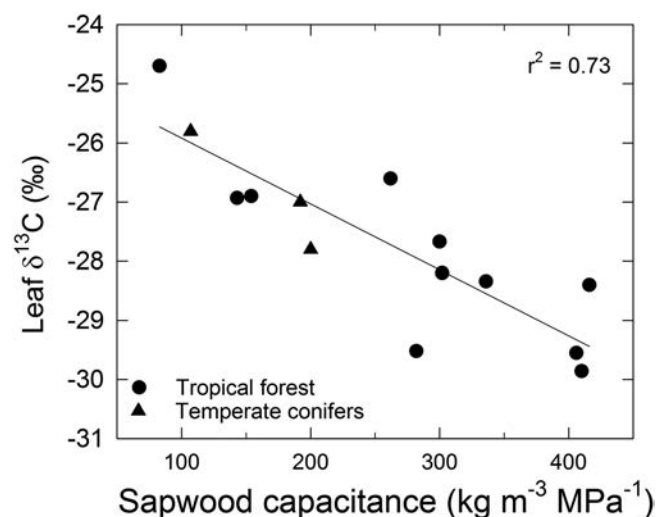


FIGURE 7 As sapwood capacitance increases, the stomatal limitation on photosynthesis declines, as indicated by the leaf $\delta^{13}\text{C}$ value across 14 tropical angiosperm and temperate conifer species. Data and sources are listed in Table S4

2003, although not always, Pivovarov, Sack, & Santiago, 2014). High leaf hydraulic conductance tends to be associated with thin leaves (Brodribb, Feild, & Jordan, 2007), which may have limited capacitive water storage volume. Finally, recent work has shown the importance of capacitance to provide structural support in flower petals (Roddy, Jiang, Cao, Simonin, & Brodersen, 2019), which are an organ whose hydraulic traits remain understudied.

The importance of capacitive stores for herbaceous species is less well understood than for woody species. The well-established trade-off between embolism resistant stems and low capacitance observed in woody tissues may not exist for herbaceous species because of differences in stem structure. Herbaceous plants can construct xylem conduits with thick walls that are able to resist embolism propagation within vascular bundles (Dória, Meijs, et al., 2018; Lens et al., 2016). However, to our knowledge, the relationship between P50 and capacitance has not been explored in herbaceous species. Another topic of potential research is whether a link exists between the capacitance and P50 of leaves. Given the reported influence of extraxylary tissues on leaf P50 values (Scoffoni et al., 2017; Trifiló et al., 2016), the link between the two parameters may not be as clear as in woody tissues.

5 | DIFFERENCES IN COORDINATION OF LEAF AND STEM TRAITS

Variability in leaf and stem vulnerability to embolism within biomes is also caused by differences in the coordination of various traits across leaves and stems. The sum of the total resistances throughout the water transport network (both apoplastic and symplastic) will determine the leaf water potential at a given soil water potential and transpiration rate. And this leaf water potential will necessarily be more negative than the water potential of the subtending stem when water is flowing distally. There are two hypotheses about the pattern of embolism vulnerability plants could exhibit to protect more basal parts of the plant, which represent greater investment in both woody and herbaceous plants. First, the vulnerability could be the same and the gradient in water potential would result in hydraulic dysfunction more readily occurring in the leaves than the stems (Zimmermann, 1983), which has been supported by some studies (Chen, Zhang, Li, & Cao, 2009; Skelton et al., 2018). Alternatively, the leaves could be more vulnerable than the stems, which would ensure leaf hydraulic failure and shut down transpiration before considerable embolisms occurred in the stems, leaving them to live another day (Tyree & Ewers, 1991). Although both hypotheses have some support, the more recent vulnerability segmentation hypothesis has been widely observed (Bartlett et al., 2016; Jin, Wang, & Zhou, 2018; Johnson et al., 2016; McCulloh et al., 2014; Rodríguez-Domínguez et al., 2018). Bartlett et al. (2016) showed that across woody dicots, the common sequence for drought responses was for leaves to reach their P50 value and TLP before stems experience their P50 value.

The segmentation of herbaceous species is far less understood than in woody species. Recently, Skelton et al. (2017) examined the

coordination of P50 values across roots, stems, and leaves of tomato plants and found little evidence for vulnerability segmentation. However, given how rarely stem and leaf P50 values have been measured in the same herbaceous species, it remains unclear if this is a widespread pattern. A further area of study is to examine the segmentation within leaves. The optical method (Brodribb, Bienaimé, & Marmottant, 2016) offers an excellent experimental approach to pursue these questions. Brodribb et al. (2016) and Skelton et al. (2017) reported that veins typically embolize from largest to smallest, but only a few species have been examined to date. Using this method on species with simpler vein networks, such as monocots or conifers, could provide further insight into their hydraulic strategies. Another area of potential research is to examine the coordination of hydraulic traits between leaves and flower petals, which are derived from leaves. Recently, Zhang and Brodribb (2017) found no differences in P50 values between leaves and flower petals in herbaceous plants but that flower petals were more vulnerable than leaves in woody species.

6 | TOWARDS A MORE PERFECT UNDERSTANDING OF “WHOLE-PLANT HYDRAULICS”

The usefulness of past studies that have focused on single organs in plant hydraulics cannot be debated. These studies have informed our understanding of plant biology, including biogeography, physiology, and ecology. However, to more completely determine the limitations and processes involved in plant hydraulics, studies must move beyond examining only one organ. Although measurements on multiple organs of mature, field-grown plants can be logistically and technically challenging, many insightful measurements can be made on juvenile plants grown in containers. Furthermore, a wide range of measurements can be made on field- or container-grown herbaceous species, and these could answer many fundamental questions about hydraulic function at the whole-plant scale. Studies that have examined scaling across multiple organs (Choat, Lahr, Melcher, Zwieniecki, & Holbrook, 2005; Johnson et al., 2016; McCulloh et al., 2014; Mencuccini et al., 2019; Skelton et al., 2017), branches and leaves (Hao et al., 2008; Johnson, McCulloh, Meinzer, Woodruff, & Eissenstat, 2011), roots and branches (Kolb & Sperry, 1999; Martínez-Vilalta, Prat, Oliveras, & Piñol, 2002), across ontogeny within branches (Rodríguez-Zaccaro et al., 2019), and from individuals to landscape-level scales (Fatichi et al., 2016; Mencuccini et al., 2019) have been very helpful for detecting and understanding coordination and trade-offs among hydraulic traits. Although anatomical measurements can be very informative, they cannot be used to fully assess hydraulic function because of differences among species in the distribution of hydraulic resistances between conduit lumen and pits and through perforation plates. Below, we briefly outline a number of potential research areas that may be particularly informative.

6.1 | In situ partitioning of whole-plant hydraulic conductance and capacitance

A number of minimally invasive techniques are available to facilitate partitioning of hydraulic properties along the soil-to-leaf continuum in intact field- or greenhouse-grown woody and herbaceous plants. In a mature, field-grown tree, for example, xylem water potential measured continuously with a stem psychrometer installed near the base of the trunk can provide estimates of dynamic variation in whole root system conductance if whole-tree sap flow is also measured near the point of psychrometer installation. The driving force for water movement through the root system can be estimated from the difference between trunk water potential at zero sap flow (water potential at the root–soil interface) and the trunk water potential corresponding to a given rate of sap flow. Pairing point dendrometers with trunk basal sap flow is another useful approach for determining below-ground hydraulic conductance (Martínez-Vilalta, Korakaki, Vanderklein, & Mencuccini, 2007). Also, below-ground electrical resistivity mapping combined with ground penetrating radar shows promise for determining root distribution and areas of active water uptake (Nadezhdina & Čermák, 2003). Strategic placement of stem psychrometers and volumetric water content sensors along the trunk to terminal branch pathway allows axial trends in conductance to be characterized along with potential dynamic variation in conductance and water storage (Hao, Wheeler, Holbrook, & Goldstein, 2013; Matheny et al., 2015, 2017; Pfautsch et al., 2018). An added advantage of this approach is that it would allow partitioning of hydraulic capacitances within and across organs. Determination of the dynamics of capacitive discharge and recharge is critical for identifying quasi-steady-state conditions under which organ and whole-plant conductances can be estimated in situ (e.g., Meinzer et al., 2003; Ward et al., 2012). For terminal portions of the pathway where leaves are attached to stems, water potentials measured with a pressure chamber on proximal and distal covered, nontranspiring leaves can be used along with sap flow measured at an intermediate point to estimate stem conductance. Additionally, electronic dendrometers installed at different locations along the axial pathway can provide information about the discharge and recharge of capacitance (De Swaef, De Schepper, Vandegehuchte, & Steppe, 2015; Salomón, Limousin, Ourcival, Rodríguez-Calcerrada, & Steppe, 2017; Scholz et al., 2008) and even serve as a proxy for the bulk water potential of the tree crown (Dietrich, Zweifel, & Kahmen, 2018). Finally, leaf hydraulic conductance and its dynamic variation can be estimated in situ if branch sap flux, branch leaf area, and the difference in water potential between covered and transpiring leaves are known (Meinzer, James, & Goldstein, 2004). The preceding and other in situ approaches may also help resolve ongoing debates over issues such as the extent to which drought-induced embolism occurs and is reversed in intact plants (Charrier et al., 2016; Rodríguez-Domínguez et al., 2018; Skelton et al., 2018), and the true shape of xylem vulnerability curves, which can differ according to the methods employed to generate and detect embolism (Cochard et al., 2010; Torres-Ruiz et al., 2017).

6.2 | What can process-based models of plant hydraulics tell us about the dynamic and vulnerable pipeline?

To develop a better understanding of how plant hydraulics affects ecosystem function, we need to scale structural and physiological traits of individual species to communities and landscapes, which requires linking leaf and canopy-level responses to climate with whole-plant water transport. It is often impossible, and probably unnecessary, to incorporate all of the details of complicated physical and biological processes into a large-scale model. Yet incorporating simplified physical mechanisms and physiological traits may be necessary to improve the predictive skills of coarse-scale models. However, few models include a representation of plant hydraulics and carbon uptake processes that is consistent with current understanding of the traits governing the exchanges of energy, water, and carbon between terrestrial ecosystems and the atmosphere (Fatichi et al., 2016). One of the greatest uncertainties in such mechanistic whole-plant water transport models had been the representation of the physiological function of roots, which had been oversimplified to the point of ignoring hydraulic transport laws. The first two models taking into account physiological integration of plant water uptake from layered soil and plant hydraulic conductance were the soil plant atmosphere model (Williams et al., 1996) and the Sperry hydraulic model (Sperry et al., 1998). More recently, several other sophisticated mechanistic models of plant hydraulic architecture were developed to predict not only the effect of root adaptations on plant water uptake and carbon fluxes but also ecosystem-level physiological characteristics under changing climatic conditions (Bohrer et al., 2005; Domec et al., 2012; Fisher et al., 2010; Heimann & Reichstein, 2008; Lorant, Mackay, Ewers, Traver, & Kruger, 2010; Mackay et al., 2003; Siqueira, Katu, & Porporato, 2008; Sperry & Love, 2015; Williams, Law, Anthoni, & Unsworth, 2001). These recent hydraulically driven soil–vegetation–atmosphere carbon and water transfer models are designed to represent processes common to vascular plants, so that the same processes (e.g., degree of anisohydry, plant loss of hydraulic capacity, and tree mortality) between species and between different biomes could be captured.

In general, root water uptake in those models is hydraulically controlled and is a function of the difference between local root water potential and local soil water potential at the root–soil interface. Water movement within the soil, needed to estimate water potential in the root vicinity, is governed by the Richards equation (Richards, 1931). In addition, the maximum flux rate of water through vegetation is determined by the difference between soil water potential and the minimum sustainable leaf water potential and by the hydraulic resistance of the soil–root–leaf pathway (Figure 4). If leaf water potential reaches the critical minimum, g_s decreases and further increases in the water loss rate are prevented (Figure 3). One assumption underlying this process is that stomatal regulation operates to minimize the effects of water stress on hydraulic conductivity (Figure 1), and by preventing the loss of plant hydraulic conductance due to xylem embolism (with or without considerations of stored water, depending on the model), carbon gained

per unit water loss over the course of a day is maximized (Huang et al., 2017). These models can include a multilayer, mixed species canopy that accounts for shoot and canopy architecture and penumbral effects, where for each layer, the model calculates gas exchange separately for each species (Ogée et al., 2009). These models can also provide insight into plant–plant interactions. For example, when species are competing for the same soil water under conditions of low water and high nutrients, then recharging internal water storage compartments is more competitively beneficial than hydraulically redistributing soil water (Huang et al., 2017). Conversely, when nutrient uptake becomes limiting, then the significance of HR in maintaining soil–root contact and microbial activities becomes more advantageous.

The main weakness of these mechanistic models is their integration processes to yield whole-plant vulnerability curves. Modelling one single organ may not accurately reflect the overall hydraulic strategy of a whole plant (Johnson et al., 2016) for the reasons we have outlined in this review. Indeed, most information on plant hydraulics comes from stems, which explains why it is the organ preferentially used as model input for proxies for overall plant hydraulic properties. However, in comparison with small roots and leaves, stems are the least hydraulically constrained organ in many species. An appropriate analogy is to consider modelling traffic patterns along roads (the xylem conduits) on a route from one village (the absorbing roots) to another (the leaves), which both have many very narrow streets (their xylem) and are connected by a super highway (the xylem of transport roots and stems). Although a lane closure (embolisms) on the highway may reduce the relatively very high speeds to some extent, it would not bring traffic to a grinding halt like a blockage in the villages. In support of this analogy, when Johnson et al. (2016) adjusted the resistance partitioning between plant organs, whole-plant hydraulic vulnerability remained essentially unaffected by branch hydraulic traits. Indeed, some models do integrate processes to yield whole-plant vulnerability by using the Ohm's law electrical analogy applied to a hydraulic circuit where all resistances to water flow are in series. This approach requires information on traits along the hydraulic continuum and the partitioning of the total plant hydraulic resistance in roots, trunk, branches, and leaves. In general, when plants are fully hydrated, it can be assumed that the partitioning of the total tree resistance in belowground and aboveground tissues each represents 50% of the whole-plant resistance to water flow (Nardini & Tyree, 1999; Cruziat, Cochard, & Améglio, 2002; RB Pratt, North, Jacobsen, Ewers, & Davis, 2010; Smith & Sperry, 2014), with the aboveground part exhibiting greater relative resistance in the leaves than in the branch and trunk (Domec et al., 2009; Sack & Holbrook, 2006). Therefore, we recommend that future studies of tree hydraulic properties focus on multiple organs, including roots and leaves, which show the greatest propensity for hydraulic failure in most species (Figure S1).

In large-scale models, the parameterization of hydraulic trait trade-offs across tissues is another way to scale tissue-level hydraulic traits to whole-plant hydraulic architecture. In Vegetation Demographics or Ecosystem models, plant water stress is typically driven only by

external factors (precipitation, VPD, and soil moisture) that downregulate water uptake and photosynthesis via uncertain empirical factors. Therefore, these models, by design, are not able to capture the wide range of stomatal and photosynthetic drought acclimation patterns (Seiler et al., 2014). Recently, the incorporation of plant hydraulic schemes that assume coordination among hydraulic traits allowed the integration of processes to yield whole-plant hydraulic parameters (Christoffersen et al., 2016; Xu, Medvigy, Powers, Becknell, & Guan, 2016). However, those models still perform poorly following quick changes in rainfall events during the dry season or when extreme droughts occur (Bonan, Williams, Fisher, & Oleson, 2014; Powell et al., 2013). Biases possibly originate from not including root distribution patterns and from a single parametrization of plant vulnerability parameters. In these recent large-scale models, the plant is represented with one value of hydraulic capacitance and P50, and it is often assumed that xylem conduits can be fully refilled following rain events (Davi & Cailleret, 2017; Xu et al., 2016). Therefore, future efforts to improve models that assume coordination among hydraulic traits should include to (a) better coordination of plant hydraulic states with stomatal functioning (Christoffersen et al., 2016; Martin-StPaul, Delzon, & Cochard, 2017; Sperry et al., 2017), (b) better characterization of the impact of hydraulic segmentation (Johnson et al., 2016), and (c) consideration of the feasibility and extent of xylem embolism refilling (Mackay et al., 2015).

These soil–root–leaf hydraulic models can also be linked to the atmosphere by the stomatal optimization theory (Katul, Palmroth, & Oren, 2009; Manzoni, Katul, & Porporato, 2014) to provide a dynamical system perspective on plant hydraulic failure (Mackay et al., 2015; Manzoni et al., 2014; Sperry et al., 2017). In those more recent approaches, the bulk water movement along the primary pathways is modelled with far finer scale spatial processes (e.g., embolism curves in each plant organ and better soil–root contact) being surrogated to nonlinearities in hydraulic properties. Hence, within each of the soil–plant compartments, the goal is to retain sufficient representation of key hydrodynamic and physiological processes while allowing for integration to the plant level. This level of complexity can potentially be increased by only using anatomical traits to predict the dynamics of embolism formation and removal under tension in xylem cells and to integrate the resulting dynamics to arrive at whole-plant vulnerability to embolism curves (Mrad, Domec, Huang, Frederic, & Katul, 2018). Furthermore, whole-plant hydraulic-based models provide unique opportunities to study the function of individual roots at depth and their effect via HR on the activity of shallow roots under various climatic conditions. Lee, Oliveira, Dawson, and Fung (2005) incorporated a simple parameterization of root HR in an atmospheric general circulation model and found that it can contribute to an approximately 40% increase in transpiration over a 3-month dry season period in Amazonia. Soil–canopy–atmosphere mechanistic models that considered HR were able to predict not only its benefits on water and carbon fluxes but also on ecosystem-level physiological characteristics such as trees' resistance to embolism and the maintenance of canopy conductance under future conditions (Domec et al., 2012; Manoli et al., 2014; Siqueira et al., 2008).

7 | CONCLUSIONS

The goal of this review has been to highlight causes of variation in single organ, particularly small-diameter branches, P50 values among co-occurring species. Other, often unmeasured, variables within the soil-to-leaf continuum drive these interspecific differences. Soil and root properties, stomatal regulation of leaf water potentials, capacitive storage, and differences in coordination of traits among organs all appear to have an impact on branch vulnerability to embolism. To fully understand limitations on species ranges (current and future), competitive interactions, and mortality, a more complete understanding of these drivers is necessary. Future research focusing on hydraulic coordination between plant organs, how differences in the rhizosphere drive changes in hydraulic traits of aboveground organs, whole-plant hydraulic approaches that identify within-plant variation in traits, the extent of phenotypic plasticity within and among populations, and process- and trait-based models representing the soil-to-leaf hydraulic pathway will be particularly informative.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1: Supplementary Information

Table S1. List of species, sampling locations, plant group types and sources of data for Figure 1. Abbreviations: RP = ring-porous, DF = diffuse-porous, CO = conifers, NW = non-woody species, Kplant = Plant hydraulic conductance (mmol m⁻² s⁻¹ MPa⁻¹), and gs-max = maximum stomatal conductance (mmol m⁻² s⁻¹).

Table S2 Notes—details of analyses performed for Figure 2.

Table S3. List of species, sampling locations, and sources of data for Figure 6. Abbreviations: Ψ_{branch} = minimum branch water potential (MPa), PDR = point of diminishing return (MPa).

Table S4. List of species, sampling locations, and sources of data for Figure 7. Abbreviations: C = capacitance (kg m⁻³ MPa⁻¹), $\delta^{13}\text{C}$ = foliar stable carbon isotope ratio (‰).

Figure S1: The distribution of 919 P50 values from 604 species, grouped by organ and ordered by decreasing median P50 (dashed lines). 92% of values came from woody species (grey) while the remainder were herbaceous (black). For each organ, the distribution of data from each ecological group is represented by the cumulative number of P50s (coloured lines), relative to the group with the most representatives. For example, it shows most leaf P50 data come from temperate deciduous forest and these P50s are fairly evenly distributed (indicated by linear increase in cumulative values). Meanwhile, few leaf P50 values exist for subtropical desert species and these tend to have more negative P50

Supplemental Information: Calculation of root to leaf (whole-tree) hydraulic vulnerability curves and simulated loss of soil-to-leaf hydraulic conductance (Figure 4).

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