

Review

Conflicting demands on angiosperm xylem: Tradeoffs among storage, transport and biomechanics

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ABSTRACT

The secondary xylem of woody plants transports water mechanically supports the plant body and stores resources. These three functions are interdependent giving rise to tradeoffs in function. Understanding the relationships among these functions and their structural basis forms the context in which to interpret xylem evolution. The tradeoff between xylem transport efficiency and safety from cavitation has been carefully examined with less focus on other functions, particularly storage. Here, we synthesize data on all three xylem functions in angiosperm branch xylem in the context of tradeoffs. Species that have low safety and efficiency, examined from a resource economics perspective, are predicted to be adapted for slow resource acquisition and turnover as characterizes some environments. Tradeoffs with water storage primarily arise because of differences in fibre traits, while tradeoffs in carbohydrate storage are driven by parenchyma content of tissue. We find support for a tradeoff between safety from cavitation and storage of both water and starch in branch xylem tissue and between water storage capacity and mechanical strength. Living fibres may facilitate carbohydrate storage without compromising mechanical strength. The division of labour between different xylem cell types allows for considerable functional and structural diversity at multiple scales.

XYLEM AND TRADEOFFS

The secondary xylem tissue of woody angiosperms has three basic functions, namely long distance water transport, mechanical support of the plant body and storage of water and nutrients (Fig. 1; Table 1). These functions are linked to different xylem cell types and xylem that is proficient at one function may necessarily be poor at another function giving rise to tradeoffs (Meinzer 2003; Pratt *et al.* 2007; Preston *et al.* 2006; Sperry *et al.* 2006). There are many xylem traits that determine resource acquisition and use. Of central importance is the role of xylem in supplying water to leaves that must lose water to acquire CO₂ through their stomata, providing a clear link between xylem supply and photosynthesis (Brodrribb & Feild 2000; Santiago *et al.* 2004). Understanding xylem tradeoffs and their structural underpinning and how xylem functions are integrated to maximize fitness

is critical for understanding the diversity in physiological, structural and life history types found among woody plant species (Ackerly 2004; Pratt *et al.* 2007).

In the context of tradeoffs, there are two common explanations for why particular traits may be linked to one another. Firstly, there are cases where structural, physical or chemical constraints govern a particular relationship and make it an unavoidable outcome of the laws that govern matter and space. For example, there is a strong relationship between tracheary element diameter and hydraulic conductivity. This relationship is an outcome of the physics of water flow through tubes and is described mathematically by the Hagen–Poiseuille equation (Hacke *et al.* 2016; Tyree *et al.* 1994; Tyree & Zimmermann 2002). Another reason why inescapable tradeoffs may arise in angiosperm xylem is related to the division of labour between the cells that comprise this complex tissue (Fig. 1). The volume available to fill with these different cell types is finite and, in a simplified scenario, having more of one cell type at the expense of another may enhance a particular function but compromise another (Bittencourt *et al.* 2016; Preston *et al.* 2006; Sperry *et al.* 2008).

A second non-mutually exclusive possibility is that associations of traits arise because they function as part of an integrated resource acquisition strategy (see reviews by Chave *et al.* 2009; Grime 2006; Reich 2014). In this case, the association is driven by natural selection in response to the environment whereby limited resources are allocated in the context of economics (Bloom *et al.* 1985; Reich 2014). The core of the leaf economics spectrum exemplifies this: long-lived leaves that have a slow photosynthetic return of carbon for a given investment of resources (carbon, nitrogen and phosphorous) contrast with shorter-lived leaves that have higher rates of photosynthetic return per investment (Wright *et al.* 2004). Identifying the mechanisms that govern relationships between traits is important for developing general predictive models of plant function and evolutionary pathways. Such models are also important for predicting ecological dynamics including ecosystem function and the effects of changing environments (Chave *et al.* 2009; Cornwell *et al.* 2009; Reich 2014; Sperry & Love 2015).

In the context of resource economics, it is important to consider the costs associated with various vascular structures and functions over time; however, there has been little research on this to date. Xylem tissue forms the bulk of most woody

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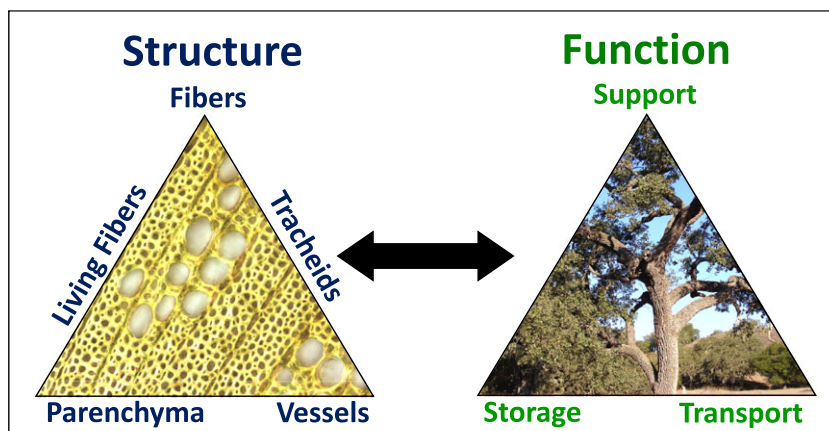


Figure 1. Different xylem cell types correspond to different xylem functions allowing for a division of labour among the cell types. Tracheids are structurally and functionally intermediate fibre and vessels. Living fibres are structurally quite different from parenchyma, but functionally lie in between the two cell types, because they provide both structural support and storage. Figure modified from Pratt *et al.* (2008b).

Table 1. Xylem traits relating to safety, efficiency, storage and mechanical support

Traits	Commonly measured parameters
Hydraulic	
<i>Safety</i>	The xylem pressure at 50% loss of hydraulic conductivity (P_{50} ; -MPa) ^a
<i>Efficiency</i>	Xylem specific hydraulic conductivity (K_s ; $\text{kg s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$)
Support	
<i>Resistance to breaking</i>	The maximum force experienced prior to breakage per second moment of area (MOR; MPa/mm^2)
<i>Stiffness</i>	Modulus of elasticity (MOE; MPa/mm)
Storage	
<i>Water</i>	Capacitance ($\Delta\text{RWC}/\Delta\text{MPa}$) or ($\text{kg m}^{-3} \text{MPa}^{-1}$)
<i>Carbohydrates</i>	Starch or non-structural carbohydrate content (g/g) or (g/m^3)

^aMany studies use other values such as P_{10} , P_{75} , P_{88} or P_{90} depending on the question being examined.

plants and the respiration rates of xylem over time are an important cost, yet there are too few data available to synthesize this aspect of the xylem resource budget in the context of xylem tradeoffs (Spicer & Holbrook 2007; Teskey & McGuire 2002). Do different tissue configurations, such as greater quantities of living cells, lead to greater respiratory demands? Are ring, diffuse and coniferous xylem types fundamentally different in such costs (Johnson *et al.* 2012)? How is respiration of xylem affected by dehydration? Is xylem density an adequate proxy for construction costs? A full understanding of these costs will be necessary to fully understand the resource economics of xylem at the tissue and whole plant scale.

In the present review, we assess xylem tradeoffs of distal branches focusing on woody vessel-bearing angiosperm species. There have been many excellent reviews and meta-analyses on various aspects of this topic (Baas *et al.* 2004; Brodribb *et al.* 2012; Carlquist 2015; Chave *et al.* 2009; Gleason *et al.* 2016; Hacke & Sperry 2001; Hacke *et al.*

2005; Lucas *et al.* 2013; Maherali *et al.* 2004; Meinzer *et al.* 2010; Pittermann 2010; Sperry *et al.* 2008). We diverge from these previous studies chiefly by highlighting tradeoffs with storage. There is a paucity of data on xylem storage, so in this review we relied heavily on previously unpublished data from our own research and a discussion of hypotheses that might form a basis for future studies.

Our focus on distal branches is more for practicality than a reflection of their chief importance over other organs or locations within the plant body. Most studies of xylem tradeoffs have focused on distal branches. Large stems and roots pose special challenges and have been far less studied in the context of tradeoffs. Plant fitness occurs at the level of the whole plant; thus, a focus on branches alone is necessarily incomplete (Meinzer *et al.* 2010; Sperry *et al.* 2008). Nevertheless, the vascular system should display considerable coordination within the plant body and the factors that govern this are of considerable interest (McCulloh *et al.* 2003; Smith *et al.* 2014). Moreover, in seasonal environments, the plant vascular system commonly comes into equilibrium with the soil water potential in the hours before dawn when transpiration is at a minimum, which means that all the tissues will experience a similar water potential when dehydrated. An exciting challenge for future studies is to more fully explore tradeoff analyses in large stems (Lachenbruch & McCulloh 2014), roots (Plavcová *et al.* 2016; Pratt *et al.* 2007), at the whole plant scale (Edwards *et al.* 2014; Meinzer *et al.* 2010; Sperry *et al.* 2008), and integration of xylem and phloem function (Lucas *et al.* 2013; Zwieniecki *et al.* 2004).

EVOLUTIONARY CONTEXT

Large multicellular organisms require an efficient and reliable transport system to move water and solutes in bulk through the body in order to maintain homeostasis (LaBarbera 1990; McCulloh *et al.* 2003; McElrone *et al.* 2003; West *et al.* 1997). Evolution of a vascular system was one of the key innovations as plants evolved from an aquatic

to terrestrial environment and subsequently radiated to fill new terrestrial niches (Bailey 1953; Pittermann 2010). Early tracheophytes evolved single-celled tracheids with thick and lignified cell walls that enabled plants to more easily grow upright, taller and evolve a broader range of structures and specialized functions (Bailey 1953). The evolution of multicellular vessels has arisen independently in several clades (Pittermann 2010), and in angiosperms this dates to approximately 135 million years ago (Sperry 2003). Fibres evolved along with vessels, and their thick walls provided structural support. The evolution of different cell types that divided the transport and support functions allowed for the evolution of a greater range of structural and functional vascular adaptations than would have been possible otherwise. The angiosperms are the dominant plant group over much of the globe in part because of their vesselled xylem and the functional and ecological diversity that it facilitates.

Woody angiosperms are widely divergent in their xylem cellular makeup (Schweingruber *et al.* 2006). For example, angiosperm xylem parenchyma in Australia taxa ranges from 3 to 64% in cross section (Pate *et al.* 1990). Other global studies find even broader ranges (Morris *et al.* 2016; Spicer 2014). The vessel volume of angiosperm tree species ranges from 6 to 55% and fibres from 26 to 76% (Gartner 1995; Panshin & de Zeeuw 1980). Moreover, the dimensions of cells and their arrangements are also highly variable (Carlquist 2001). Diversity in xylem structure is intriguing and has important implications for early evolution of vessels as well as tradeoffs between structure and function (Fig. 2).

XYLEM FUNCTIONAL TRAITS AND THE SAFETY-EFFICIENCY TRADEOFF

There are many xylem traits and relationships between traits that are important to examine in the context of tradeoffs (Table 1 provides some common examples). The xylem supplies water to leaves that must lose water to acquire CO₂. The xylem must also provide a reliable or 'safe' supply of water to leaves and living cells; thus, it needs to resist failure by avoidance or tolerance mechanisms. The xylem of branches supports a leafy canopy display, as well as flowers and fruit; thus, it has to be mechanically reinforced to avoid drooping or breakage. Finally, the xylem stores resources (water, carbohydrates and nutrients) to adjust to variations in supply and demand of these resources. More than any other tradeoff, the relationship between xylem safety and efficiency has been a focal point of research, and we start with a brief review of this topic.

Xylem efficiency is a key trait in the context of resource economics. Xylem efficiency is commonly expressed as hydraulic conductivity (volume flow rate/ pressure gradient) per unit xylem or sapwood area (K_s) (Table 1; Tyree & Ewers 1991). The advantages of efficient xylem are that the water lost via transpiration (E) can be readily replaced ensuring that leaf water deficits are minimized and that stomata stay open and do not limit diffusion of CO₂ to the chloroplasts. Thus, for a given leaf area, higher rates of E can be achieved in xylem with increased efficiency or the same E can be achieved with thinner stems leading to reduced investments in xylem tissue (Gleason *et al.* 2016). For a given stem diameter, greater leaf area can be supported with the same E for more efficient species.

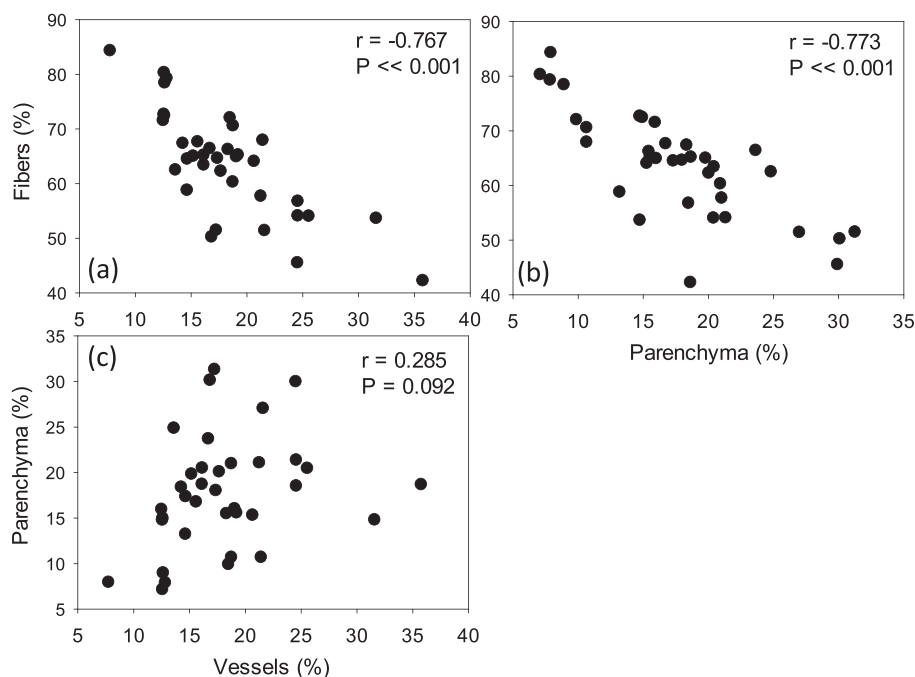


Figure 2. The relationships between different cell types in cross section of branches. Fibre abundance is negatively correlated with both vessel (a) and parenchyma abundance (b), whereas vessel and parenchyma abundance are not correlated (c). Unpublished data are from 36 southern California chaparral shrub species.

Moreover, for a given driving force, a volume of water can be transported greater distances in efficient xylem (Bittencourt *et al.* 2016). Lianas that parasitize co-occurring woody plants for mechanical support represent the fullest expression of some of these advantages. This growth form can achieve very high K_s values with long and skinny stems that supply large leaf areas (Ewers *et al.* 1990; Gartner 1991; Patiño *et al.* 1995; Zhu & Cao 2009).

Another important xylem trait relates to the ability to sustain water transport in response to environmental stresses. Cavitation is the chief form of transport failure, and it occurs when water in vessels is displaced by gas, forming blockages or emboli. This is problematic because embolized conduits cannot transport water; thus, xylem hydraulic efficiency is reduced. Cavitation is a threat to plants because xylem sap has limited stability as it is under tension (Dixon & Joly 1895). Cavitation can occur when water demand outstrips supply and deficits push xylem tensions beyond critical points of failure and gas seeds into functional conduits as might happen during a drought. Cavitation can also be nucleated by freeze–thaw stress (Sperry *et al.* 1994), mechanical damage (Jacobsen *et al.* 2005), fire (Michaletz *et al.* 2012; West *et al.* 2016) or from pathogens (Tyree & Zimmermann 2002).

The importance of cavitation resistance in the context of drought resistance is evidenced by the relationship between cavitation resistance and the minimum seasonal water potential a species experiences (Fig. 3). This relationship suggests that cavitation resistance is often coordinated with the level of dehydration experienced in nature. Presumably, having xylem that is more resistant than necessary incurs unnecessary costs and having xylem not resistant enough leads to lethal levels of cavitation and embolism. These costs come in the form of greater investment in denser tissues that includes thicker vessel walls (to resistant implosion of vessels) and greater xylem density (Hacke *et al.* 2001; see biomechanics section below). Another cost is reduced xylem efficiency. Key ways that plants achieve high efficiency are through

wide diameter vessels, thin pit membranes with wide pores and vessels with a lot of pit area, all of which are traits that compromise safety (Choat *et al.* 2008; Lens *et al.* 2011; Sperry & Hacke 2004). Consequently, the chief explanation for why efficiency is limited is because it comes at the cost of xylem safety from cavitation

The evidence for a tradeoff between safety and efficiency is consistently supported by data showing that no species has evolved both high resistance to cavitation and high K_s (Fig. 4; Gleason *et al.* 2016; Tyree *et al.* 1994). Moreover, there are well understood structure–function relationships associated with this tradeoff. There is a strong negative relationship between vessel diameter and vessel frequency (Fig. 5a; Sperry *et al.* 2008). Wide vessel diameters are important for achieving the highest levels of efficiency (Fig. 5b), while high vessel frequency is important for safety because it reduces the overall impact of cavitation in a single vessel (Ewers *et al.* 2007; Tyree & Zimmermann 2002) and there is a positive relationship between transport safety measured as cavitation resistance and vessel frequency (Fig. 5c). Wide diameter vessels can only achieve high efficiency if they have porous pits, and this leads to a structural basis for a tradeoff between safety and efficiency at the level of the pit membranes (Choat *et al.* 2008; Jarbeau *et al.* 1995; Meyra *et al.* 2007). Vessels could also achieve high efficiency by increasing the pitted area of vessel surfaces, rather than the characteristics of individual pits (Sperry & Hacke 2004); however, this also seems to increase risk. Species widely differ in the area of vessels that are pitted and those that have high pit areas tend to be more vulnerable to cavitation. This pattern is referred to as the ‘rare pit hypothesis’ (Hargrave *et al.* 1994; Wheeler *et al.* 2005).

Because of their central importance in plant hydraulics, pit membranes continue to be a focal area of research. Pit membranes are materially similar to primary walls, and important research is examining differences in chemical composition of pit membranes (Gortan *et al.* 2011; Schenk *et al.* 2015; Schmitz *et al.* 2012) and diversity in

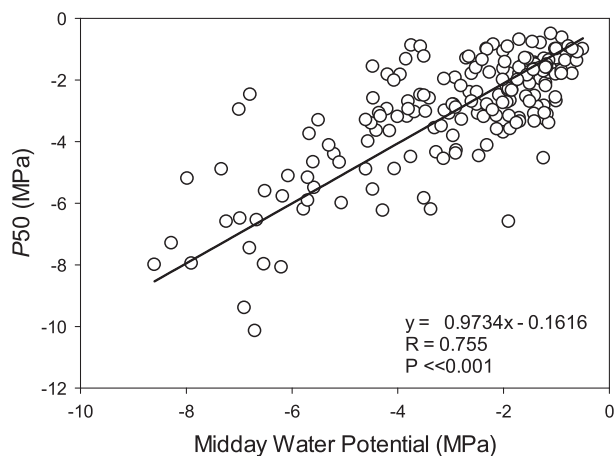


Figure 3. Minimum seasonal midday water potential plotted as a function of cavitation resistance (P_{50}) for branches of 191 angiosperm species (data from Choat *et al.* 2012). Best fit line is from SMA regression, and the slope is not different from 1 (0.97 ± 0.10).

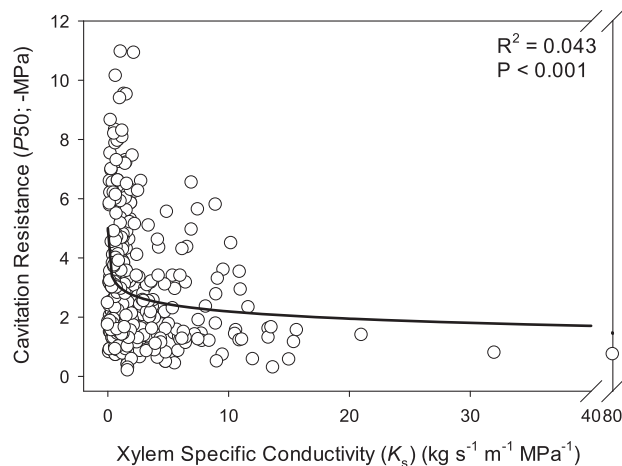


Figure 4. Plot of xylem safety (P_{50}) as a function of xylem efficiency of branches of angiosperms. Solid line is a best logarithmic fit. Data plotted are modified from Choat *et al.* (2012); Gleason *et al.* (2016) and Pausas *et al.* (2016).

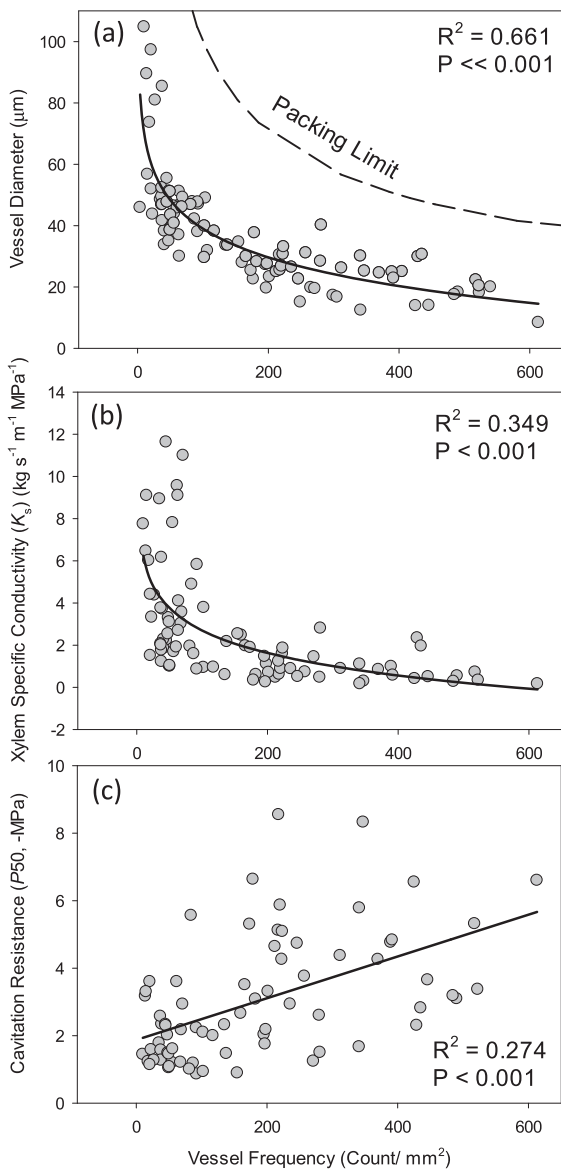


Figure 5. Plot of vessel diameter (a), xylem efficiency (b) and cavitation resistance (c) as a function of vessel frequency for branches. Solid lines are best logarithmic fit (a and b) and a non-log linear fit (c). The dashed line in panel a represents the packing limit that is calculated as if the entire area of xylem were composed of vessels that are the mean diameter for the species. Data plotted are from multiple studies (Chen *et al.* 2009; Choat *et al.* 2005; Pratt, unpublished data, Choat *et al.* 2007; Edwards 2006; Gartner 1991; Iovi *et al.* 2009; Martinez-Vilalta *et al.* 2002; Trifilo *et al.* 2007; Vander *et al.* 2000; Zotz *et al.* 1997).

pit membrane characteristics (Dute 2015; Jacobsen *et al.* 2016; Li *et al.* 2016; Schulte *et al.* 2015). Pit membrane thickness, shallower pit chambers and relatively smaller pit apertures that would reduce the strain on an aspirated pit membrane appear to be important in affecting safety (Lens *et al.* 2011). Moreover, a cross-species comparison found that greater pit membrane thickness was associated with greater resistance to cavitation because of dehydration (Li *et al.* 2016).

A recent meta-analysis assessed the tradeoff between safety and efficiency and found that there is not a strong correlation between these two traits (Fig. 4; Gleason *et al.* 2016). The most perplexing result found by this and numerous other studies is that there are many species that have both low safety and low efficiency (bottom left corner in Fig. 4; Gleason *et al.* 2016; Maherali *et al.* 2004; Tyree *et al.* 1994). Explaining why these species are so abundant and represented in many different environments is a significant challenge to our understanding of plant vascular systems. A key question is why all species are not maximizing their efficiency for a given level of safety among species that have low to moderate safety levels.

One explanation for this observation is that some species may refill embolized conduits; thus, they do not need to have high resistance to cavitation. Some plants can refill embolized xylem conduits by pressurizing the vascular system when transpiration is halted (Sperry *et al.* 1987; Tibbets & Ewers 2000), and some plants may refill when xylem pressures are negative (Bucci *et al.* 2003; Hacke & Sperry 2003; Salleo *et al.* 1996), which has been difficult to explain mechanistically (Zwieniecki & Holbrook 2009). Refilling cannot fully explain the existence of many species with low levels of cavitation resistance because it still does not explain why they would have low efficiency. Moreover, not all species have the capacity to refill embolized xylem either by positive pressure or under negative pressure (Clearwater & Clark 2003; Knipfer *et al.* 2015a), even among congeneric species (Knipfer *et al.* 2015b); moreover, dehydration and freeze/thaw stresses can damage pit membranes rendering refilling futile in situations where stress is chronic (Christensen-Dalsgaard & Tyree 2013; Hacke *et al.* 2001; Hillbrand *et al.* 2016; Li *et al.* 2016), although it is possible that some species may be able to repair damaged pit membranes (Christensen-Dalsgaard & Tyree 2014; Stiller & Sperry 2002). For many species in seasonal environments, the only way to restore full transport capacity following cavitation is to grow new xylem when conditions permit (Hacke & Sauter 1996). For these species, resisting xylem cavitation by adaptations that allow high xylem tensions to occur while avoiding cavitation is crucial (Maherali *et al.* 2004; Pratt *et al.* 2008a).

Ecophysiology of low safety and low efficiency: an example

Some species might have low safety and efficiency because of ecological and evolutionary factors. In this context, it is necessary to consider the selective forces acting on safety and efficiency. Many species appear to adjust their safety levels to the minimum water potential they experience in nature (Fig. 3); however, this does not mean that these water potentials are the ultimate force selecting for a particular level of safety. The critical question is do species that are more cavitation resistant, and dehydration tolerant, have higher survival during drought, that is, are they more *drought resistant*? There are very few studies that have directly examined this in an ecologically relevant way (Kursar *et al.* 2009; Pratt *et al.* 2008a; Tyree *et al.* 2003), and both dehydration tolerance and dehydration avoidance mechanisms are viable pathways to drought resistance (Garcia-Forner *et al.* 2016; Lopez-Iglesias *et al.* 2014; Mitchell

et al. 2013; Padilla & Pugnaire 2007; Pineda-Garcia *et al.* 2013; Venturas *et al.* 2016).

One study of nine species of evergreen chaparral shrub seedlings found that higher survival was associated with higher resistance to cavitation among eight species; however, a ninth species, *Frangula californica* (formerly *Rhamnus*), also had relatively high survival, but was not cavitation resistant (Fig. 6a). This species avoided extreme tissue water deficits by having a higher root to shoot ratio, which led to a more favourable water status at the peak of the drought (Fig. 6a, b). This illustrates that cavitation resistance is only one means of drought resistance and that other adjustments that allow plants to avoid lethal water deficits can lead to successful trait combinations that include less safe xylem.

The case of *F. californica* is informative because this species also had the lowest xylem efficiency, measured at multiple scales (Pratt *et al.* 2010), and thus it represents a species that combines low safety and low efficiency. For species with this trait combination, the tradeoff between safety and efficiency is likely not the only factor influencing K_s and cavitation resistance. The combination of traits that a species displays is determined by its resource use characteristics in what has been referred to as the fast–slow continuum. ‘Fast’ species acquire and use resources quickly and ‘slow’ species do this more slowly. Consistent with lower xylem efficiency, *F. californica* also had the lowest maximum stomatal conductance and photosynthetic rates indicating that it is closer to the slow end of the continuum than the other species (Fig. 7; Pratt *et al.* 2012; Pratt *et al.* 2010). It seems likely that *F. californica* avoids tissue water deficits and maintains functionality longer into a drought than the other species, albeit operating at a lower level of maximum performance. This species’ growth capacity in full sun was not significantly diminished compared to the other species, and this

was accomplished through a range of other physiological adjustments (Fig. 7d; Pratt *et al.* 2012). In the shade, it performed much better than the other species, including growth and survival of drought (Pratt *et al.* 2012), and it is its shade adaptations that probably make this a ‘slow-adapted’ species (Grubb 1998).

The fast–slow continuum represents an important model describing how natural selection and tradeoffs have led to predictable trait combinations found among a wide range of species. Fast species should have high xylem transport efficiency and slow species should have low efficiency; however, cavitation resistance does not integrate into this spectrum in a simple way. Fast species cannot have high cavitation resistance, yet slow species might have high or low cavitation resistance as the data for *F. californica* illustrate. In summary, we predict that species combining low xylem safety with low xylem efficiency are species that fall into the slow end of the fast–slow continuum and they are species that have traits or ecologies that allow them to avoid dehydration of their tissues or they have mechanisms to tolerate (e.g. leaf shedding, dormancy, ionic adjustments to sap) or repair embolism that occurs (Ogasa *et al.* 2013; Trifilò *et al.* 2014). One area for future research is merging the study of drought resistance traits in the context of both the fast–slow continuum and the safety versus efficiency tradeoff.

Scaling: safety and efficiency

A full understanding of the safety versus efficiency tradeoff must take into account the important issue of scale. There are many factors that can affect this relationship when moving from the level of individual pit membranes or vessels up to tissues composed of vessel networks to the whole plant (Jacobsen *et al.* 2016; Lachenbruch & McCulloh 2014; Sperry *et al.* 2008). For example, when scaling from individual pits to bulk xylem

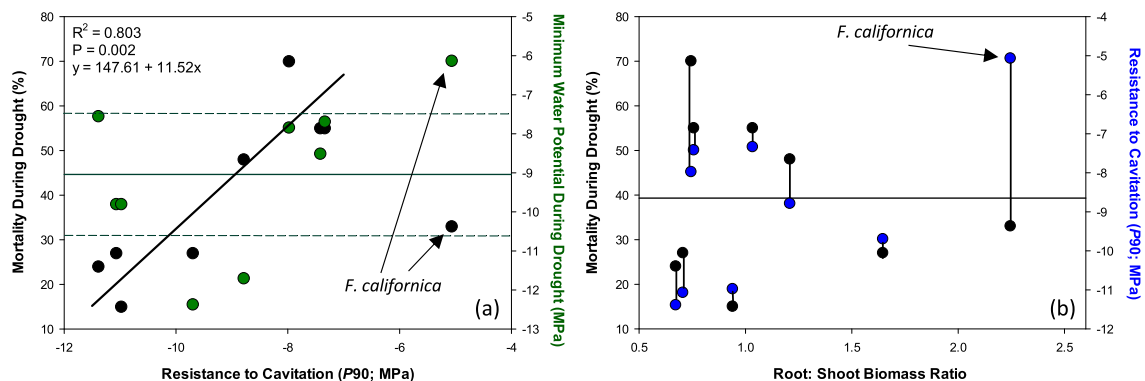


Figure 6. Plot of seedling mortality during drought (black symbols and primary y-axis) as a function of resistance to cavitation (a). Also plotted is the minimum seasonal water potential experienced by plants during the drought (green symbols and secondary y-axis) as a function of cavitation resistance (a). The solid green line is the mean for minimum seasonal water potential and the upper and lower green dashed lines mark the 95% confidence limits. The best fit line is an SMA regression for the species that experienced the most tissue dehydration during the drought, that is, those species within or below the mean measured water potential during the peak of the drought. One species, *Frangula californica*, was an outlier that experienced significantly less tissue dehydration than the other species and had low mortality for its level of cavitation resistance. Panel (b) shows mortality (black symbols and primary y-axis) plotted as a function of root:shoot biomass with resistance to cavitation on the secondary y-axis (blue symbols). The horizontal line in panel b indicates the mean mortality across all species. Species with mortality below the mean either had high cavitation resistance (bottom left) or high root:shoot ratio (bottom right). The lines connect the mortality and resistance to cavitation for each species. Cases where black symbols are greater than blue symbols indicate higher mortality for a given level of cavitation resistance and vice versa for when blue symbols are above the black symbols. Note that *F. californica* had a large difference between resistance to cavitation and mortality indicating low mortality for its level of cavitation resistance. Data are from Pratt *et al.* (2009, 2010, & 2012).

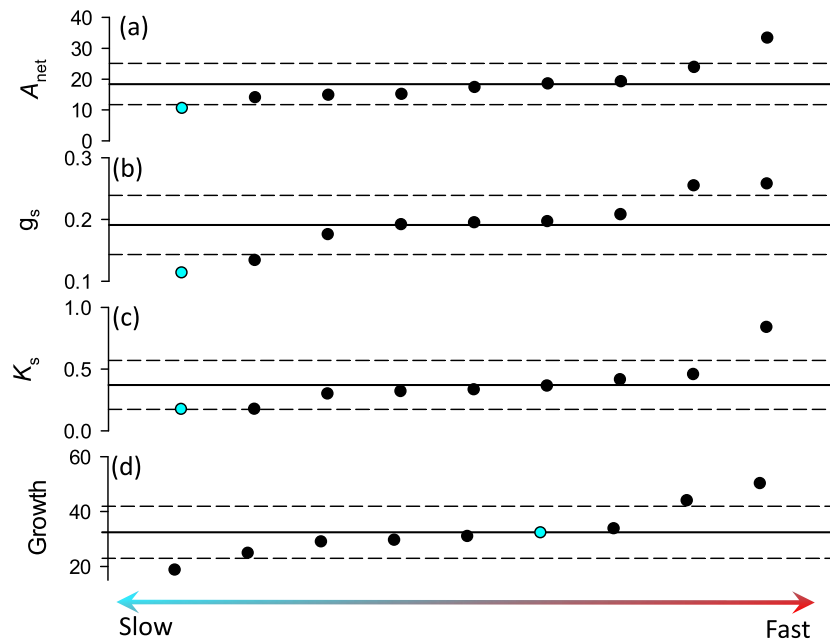


Figure 7. Key resource acquisition and use traits, including net carbon assimilation (A_{net} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), stomatal conductance (g_s ; $\text{mol m}^{-2} \text{s}^{-1}$), xylem specific conductivity (K_s ; $\text{kg s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$) and biomass produced during a growing season (growth; g) for nine species of chaparral shrub seedlings from a semi-arid common garden in southern California. Within each panel, the solid line is the mean for all species, and the dotted lines represent the upper and lower 95% confidence limits. For each panel, species values are arranged in the order of low to high, so species order is variable among panels. Values were measured during the growing season and are thus maximum values. *Frangula californica* is marked with a cyan symbol. Low values for these traits represent slow resource acquisition for water and carbon and vice versa for high values. Data are from Pratt *et al.* (2008, 2010, and 2012).

tissue, an increase in efficiency without changing safety is possible by simply increasing the vessel frequency. Likewise, in going from individual vessels to vessel networks, there are a number of factors that will alter safety and efficiency such as, how sectorised or connected the vessels are, both of which affect embolism spread (Carlquist 2009; Ellmore *et al.* 2006; Loeper *et al.* 2007; Scholz *et al.* 2013), non-randomly distributed short vessels (Brodersen *et al.* 2013) and the presence of tracheids (Carlquist 1985; Pratt *et al.* 2015). Tracheids should have a large effect on the vessel-to-vessel pitting in species with vasicentric tracheids and how this affects xylem safety in the context of the rare-pit-hypothesis is an open question (Hacke *et al.* 2009). At the scale of the whole plant, there are many poorly understood factors affecting safety and efficiency, and research into this represents a significant challenge for future studies (Lachenbruch & McCulloh 2014; Meinzer *et al.* 2010; Sperry *et al.* 2008).

BIOMECHANICS

Mechanical support of xylem is important at many scales with implications for both safety and efficiency. Water transport under negative pressure exposes xylem vessel pairs to hoop and bending stresses (transport stress) that would lead to cell collapse if the cell wall thickness (t) to lumen diameter (b) ratio was not great enough (Hacke *et al.* 2001; Niklas 1992; Sperry & Hacke 2004). Vessel collapse can occur in woody tissues (Schweingruber *et al.* 2006), and it is readily observed in cells

that lack a robust supporting matrix, such as in leaf tracheids (Brodrribb & Holbrook 2005; Cochard *et al.* 2004). Estimated resistance to vessel collapse $(t/b)^2$ is positively correlated to cavitation resistance and minimum seasonal water potential (Hacke & Sperry 2001; Jacobsen *et al.* 2007a; Lens *et al.* 2011; Pratt *et al.* 2007). However, numerous studies have failed to find these correlations (Fichot *et al.* 2010; Jacobsen *et al.* 2007b). Nevertheless, the critical issue is that vessels have a high enough $(t/b)^2$ value to avoid vessel implosion (Hacke *et al.* 2001; Pittermann *et al.* 2011), and this seems to generally be the case.

The need to resist implosion under tension means that the mechanical and transport functions of xylem are interdependent. This is certainly so in tracheid-based systems where the tracheids both transport water and provide mechanical support (McCulloh *et al.* 2004; Pittermann *et al.* 2006). In angiosperm xylem the division of labour between fibres for support and vessels for water transport mitigates interdependency (Fig. 1). Nevertheless, xylem safety from cavitation is positively correlated with more robust tissues including strength (modulus of rupture; MOR), stiffness (modulus of elasticity; MOE) and xylem density (Jacobsen *et al.* 2005; Jacobsen *et al.* 2007c; Pratt *et al.* 2007). Tissue-level mechanical properties, including xylem density, are dominated by fibre traits suggesting that fibres are involved in this association (Jacobsen *et al.* 2005; Martínez-Cabrera *et al.* 2009; Ziemińska *et al.* 2013). The link between xylem transport safety (cavitation and implosion resistance) and xylem density and mechanical support of the plant body

represents a cost of safe transport in the form of thick walled vessels and fibres (Hacke *et al.* 2001).

Mechanical support may be at odds with efficient transport for multiple reasons, particularly at the cell or vessel level. For a single vessel, greater hydraulic efficiency is associated with wider conduit lumens and greater pit areas both of which reduce mechanical strength. At the stem level, there is some evidence of a tradeoff between biomechanics and efficiency from intraspecific studies. For example, the K_s of climbing vines was greater than free standing ones when compared intraspecifically (Gartner 1991). Mechanically perturbing hybrid *Populus* clone stems led to a reduction in K_s , vessel area, and an increase in xylem density and stiffness compared to un-perturbed controls (Kern *et al.* 2005). Intra-plant comparisons have also found that in regions where mechanical strain is high conductivity is reduced (Christensen-Dalsgaard *et al.* 2007). The clear intraspecific associations between tissue mechanics and efficiency suggest that the two functions are linked such that intraspecific plasticity cannot generally overcome this constraint (however see Gartner *et al.* 2003).

In contrast, the division of labour between vessels and fibres may uncouple the mechanical versus hydraulic efficiency tradeoff of xylem at the tissue level. Studies comparing across species have found no evidence for an efficiency versus mechanical strength tradeoff in stems (Poorter *et al.* 2010; Pratt *et al.* 2007; Woodrum *et al.* 2003; Zhang *et al.* 2013) with some studies finding weak support based on analyses lacking phylogenetic information (Gleason *et al.* 2012; Markesteijn *et al.* 2011). There is no clear mechanistic reason why tissue strength should be directly at odds with tissue hydraulic efficiency. Vessel-based systems must have some fibres for support; thus, there is a vessel packing limit that may underlie a tradeoff in environments where diameter of vessels is limited by freezing and drought (Fig. 4; Hacke *et al.* 2006; Hacke *et al.* 2016; Sperry *et al.* 2008). However, vessel frequency and mechanical strength are not correlated even when data are limited to species with diameters below the freezing vulnerability threshold (Pratt, unpublished data). Mechanical strength of fibres can be modulated in many ways such as by modifications to their arrangement and cellulose microfibril angle (Reiterer *et al.* 1999), cell wall to lumen ratio and cell wall chemistry; thus, there is a wide range of evolutionary options to modify stem mechanical strength (Carlquist 2014; Panshin & de Zeeuw 1980). The uncoupling of mechanics and transport efficiency is consistent with hypothesized advantages of vessel-based xylem evolution allowing vesselled species to achieve greater maximum efficiency while maintaining other functions.

XYLEM STORAGE

Although storage is an important xylem function (Kozlowski & Pallardy 1996), research has more often focused on transport and biomechanics. Thus, we currently lack information on how xylem storage, particularly carbohydrate storage, integrates with the water transport and mechanical support functions of xylem. Here we firstly examine capacitance, and next we consider carbohydrate storage. A hypothesis motivating such comparisons is that the need for xylem storage has been

an important evolutionary driver of xylem structure and function in woody plants.

Capacitance

Storage of water is an important factor affecting plant resource use (Waring & Running 1978). Water storage, or capacitance, is expressed as change (Δ) in tissue relative water content (RWC) for a given change in tissue water potential (Ψ) (Domec *et al.* 2006) and is expressed as

$$\Delta\text{RWC} / \Delta\Psi. \quad (1)$$

In this equation $\text{RWC} = (\text{fresh weight} - \text{oven dry weight}) / (\text{saturated weight} - \text{oven dry weight})$.

More commonly, capacitance has been expressed as the mass of water released per volume of xylem tissue per $\Delta\Psi$ ($\text{kg m}^{-3} \text{MPa}^{-1}$) (Holbrook 1995). The $\Delta\text{RWC} / \Delta\Psi$ provides information on water released from tissues relative to a fully hydrated state. The latter term provides a measure of the absolute amount of water released from a given volume of tissue. Measurements of capacitance typically involve saturating tissues with water and weighing them to get the saturated weight followed by dehydrating tissues and measuring their mass and Ψ as they dehydrate to generate a pressure volume or moisture release curve (Fig. 8). Water may be stored in the xylem or the bark, but the xylem is a much larger storage reservoir (Scholz *et al.* 2007). The inner bark is also a source of water that can feed the xylem via ray parenchyma networks (Pfautsch *et al.* 2015a). In cases where xylem tradeoffs are the chief focus of a study, capacitance in the xylem alone can be determined in debarked and de-pithed tissue to isolate the xylem (Pratt *et al.* 2007).

The role of capacitance in small stems of woody plants is that it can buffer tissues from large short-term drops in water potential such as might occur over the course of a sunny dry day (Meinzer *et al.* 2009; Meinzer *et al.* 2008; Scholz *et al.* 2007). In this way, capacitance is similar to high K_s , which can achieve the same result (Sperry *et al.* 2008). Because the amount of water stored in woody branches is small relative to active transpiration rates, longer term water deficits in seasonal environments cannot be overcome with capacitance in small trees and shrubs, but are important in trees that have a large bole with substantial water storage capacity (Phillips *et al.* 2003; Tyree & Yang 1990); additionally, species with considerable succulence rely on capacitance to resist drought (Nobel 1977). Woody roots typically have higher capacitance than stems (Johnson *et al.* 2013; Jupa *et al.* 2016).

Analyses of moisture release curves provide insight into the structural basis for capacitance (Tyree & Yang 1990). A slope of the initial portion of the curve comes from water stored in the small spaces between cells, which is known as capillary storage (Fig. 8a). Capillary storage typically represents the largest volume of stored water and analyses of capacitance often focus on this portion of the curve. Capillary storage represents water that is available at relatively high water potentials (0 to -0.2MPa) being largely depleted by about -0.5MPa (Tyree & Yang 1990). In some cases, other

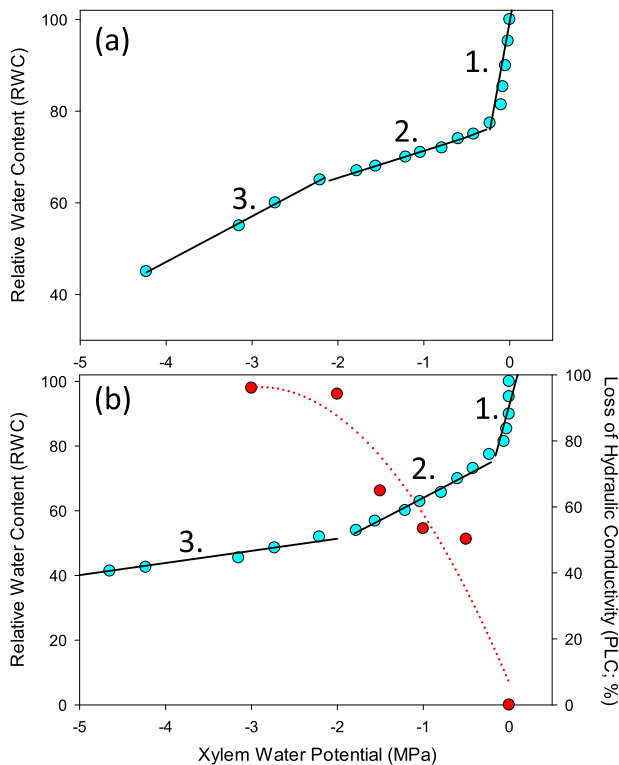


Figure 8. Relative water content plotted as a function of water potential of branch xylem tissue showing different numbered phases (cyan dots and solid black lines). The lines are best fits of different regions of the curve that are often associated with different compartments releasing water. Line 1 is interpreted as release of capillary stored water, line 2 is elastic storage and line 3 is water released from vessels that cavitate. Panel a shows a hypothetical moisture release curve. Panel b shows a similar plot of data from xylem of *F. californica* branches. On the secondary y-axis in panel b is plotted the loss of hydraulic conductivity for branches representing vulnerability to cavitation of vessels (red dots and red dotted line). There appears to be three phases of moisture release from the tissue, but the vulnerability curve shows that considerable cavitation is occurring during both phases one and two. In this curve, phase 1 would correspond to unbound water where RWC changes and water potential does not and some capillary storage. This water would be in open vessels, damaged and non-functional vessels (fatigued vessels), and intercellular spaces. Phase 2 consists of cavitation and presumably elastic storage, and phase 3 is post-cavitation tightly bound water. It is possible that data generated as in panel b have only two distinct phases especially when the unbound water is scaled out.

portions of the moisture release curve may be of interest, and they represent different compartments of xylem storage (Fig. 8a). Water is also stored elastically in tissues as they shrink and swell with access to water and can be assessed from a moisture release curve in some cases (Fig. 8a). The volume of elastic storage in woody tissues will generally be small (Sevanto *et al.* 2002; Tyree & Zimmermann 2002). Finally, the water in the lumens of tracheids and vessels may be viewed as a compartment for water storage as they release their water content when they undergo cavitation (Holttta *et al.* 2009; Lo & Salleo 1992; Tyree & Yang 1990; Vergelynst *et al.* 2015). This form of ‘cavitation storage’

comes at the cost of a loss in transport efficiency unless the vessels can be refilled (Domec *et al.* 2006; Taneda & Sperry 2008).

The anatomical basis of water storage is critical for evaluating tradeoffs with structure and function, yet methodological difficulties hamper a complete analysis (Fig. 8b). Capillary stored water comes out of spaces in between cells and cell lumens; thus, water stored in this compartment is strongly associated with lumen space, particularly of fibres (Jupa *et al.* 2016; Pratt *et al.* 2007). As larger fibre lumens are associated with lower xylem density, this leads to an inverse relationship between capillary water storage capacity and xylem density (Fig. 9a; Jupa *et al.* 2016; Pratt & Black 2006; Pratt *et al.* 2007; Stratton *et al.* 2000). The elastic storage should be related to parenchyma cell wall thickness and the amount of parenchyma in the tissue (however, see Jupa *et al.* 2016). Thus, in woody stems, this tends to be a small amount of water storage (Sevanto *et al.* 2002), where succulent stems may have large elastic capacitance volumes. Elastic and cavitation storage have not been commonly separated in studies that would allow an analysis of their functional significance or anatomical basis (Jupa *et al.* 2016; Vergelynst *et al.* 2015). Cavitation storage should contribute in a manner consistent with a species’ vulnerability curve (Fig. 8b). Most of the available data on capacitance of woody tissues comes from small segments of woody tissue (1–4 cm long) that can fit into small psychrometer chambers (however, see De Swaef *et al.* 2015; Vergelynst *et al.* 2015). In small samples, where vessels are cut open, separating capillary, elastic and cavitation capacitance is challenging (Fig. 8b; Jupa *et al.* 2016). In some cases, the amount of water in cut vessels may be calculated and removed from analyses (Jupa *et al.* 2016), or curves can be scaled to remove the portion where unbound water is released, that is, where RWC changes with no change in water potential. When this is done, it results in a two phase curve instead of the three shown in Fig. 8b. However, even these adjustments cannot fully remove artifact from the calculated values in the sense that the adjusted values will likely differ from capacitance of intact tissues. Developing new methodological approaches is needed to address this challenge (Tyree & Yang 1990). One area that is promising is the use of dendrometers (Cocozza *et al.* 2015; De Swaef *et al.* 2015; Zweifel *et al.* 2014). Moreover, *in vivo* imaging methods may prove valuable for separating the contribution of fibre and vessel stored water during dehydration (De Schepper *et al.* 2012).

There are reasons why xylem storage likely interacts with xylem transport and biomechanics. Because capillary water storage is largely influenced by fibre traits, including fibre lumen diameter and fibre lumen area (% in cross section), that is, at both the cell and tissue levels (Pratt *et al.* 2007), it should lead to a tradeoff between mechanical strength and capacitance and indeed this is the case (Fig. 9b). The link between capacitance and mechanical strength is likely driven by the association between xylem density and mechanical strength of the tissue (Fig. 9a).

With respect to water transport safety, water released from sapwood storage during the day prevents stem sapwood from

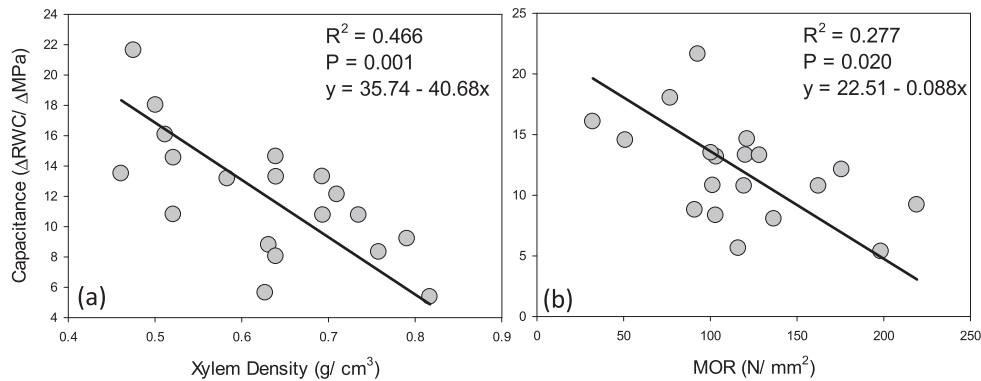


Figure 9. Plot of capacitance as a function of xylem density (a) and resistance to mechanical breakage (modulus of rupture; MOR) (b). Data are from debarked and de-pithed branch xylem tissue and the capacitance is largely capillary water storage (phase 1 with unbound water removed). The lines are SMA best fits for the data. Data are from chaparral shrubs collected at field sites in southern California (Pratt, unpublished data).

reaching highly negative water potentials during transpiration that may influence cavitation (Meinzer *et al.* 2009). Indeed, species with high stem capacitance maintain less negative midday stem water potentials than those with lower capacitance (Meinzer *et al.* 2009). Moreover, there is an inverse relationship between xylem cavitation resistance and capacitance of branches (Meinzer *et al.* 2008; Pratt *et al.* 2007). Having high capacitance may be linked to greater risk of xylem implosion supported by the negative relationship between $(t/b)^2$ and capacitance (Pratt *et al.* 2007).

Capacitance and transport efficiency may also be associated. More voluminous vessels would contribute to greater efficiency and greater capacitance of vessels when they undergo cavitation. Vessel refilling that has been documented in many studies where vessels cavitate and embolize during the day and refill by morning represents a form of capacitance (Taneda & Sperry 2008; Zwieniecki & Holbrook 1998). This release of water may lead to significant carbon gains by buffering leaf water status during the growing season (Hölttä *et al.* 2009). At least one study did not find a correlation between capacitance and transport efficiency (Pratt *et al.* 2007).

With a larger data set, we also find no relationship between capacitance and maximum K_s and or with K_s and vessel volume (mean vessel diameter² × vessel length). There are two reasons for this: firstly, fibres dominate the capacitance of tissue and thus vessels have little impact. Secondly, artifacts associated with measuring capacitance in small tissue samples hamper analysis of vessel characteristics and capacitance. Another possible connection may arise because of the presence of abundant living (developing) vessels in some species like *Vitis vinifera* (Jacobsen *et al.* 2015). In this case, these vessels might contribute to a large volume of elastic capacitance in *Vitis* spp. that have relatively wide diameter vessels that are also relatively long (Sevanto *et al.* 2002; Zweifel *et al.* 2014). In summary, there may be a positive association between capacitance and hydraulic efficiency; however, data using larger xylem samples will be needed to fully evaluate this.

Storage of carbohydrates

Xylem sapwood of stems and roots is also an important storage tissue for carbohydrates (starch and fructans; Chapin *et al.* 1990; Kozłowski & Pallardy 1996; Plavcová & Jansen 2015). Such nutrients can be stored in the xylem in ray and axial parenchyma, and living fibre cells found in some species (Esau 1965; Sauter & van Cleve 1994). Carbohydrates can also be stored in the bark, but the focus here is to assess the simplified case of carbohydrate storage in branch xylem and its effect on other xylem functions. The xylem sapwood is important to consider as it generally represents the largest volume of continuous storage in stem and root tissue (Wurth *et al.* 2005). There are additional functions of living cells in the xylem such as radial and axial transport, maintenance of the transport system (vessel refilling), defence against pathogens and wound responses (Pfausch *et al.* 2015b). All of these functions will be connected to carbohydrates in some way as they are active processes.

There are different factors that contribute to carbohydrate content of tissues that relate to allocation of resources and source–sink dynamics. If sinks are limited more than photosynthesis, carbohydrates may accumulate in tissues because they have nowhere else to go (Chapin *et al.* 1990). By contrast, storage is considered an allocation of carbohydrates to tissues for later use. In this case, allocation of carbohydrates is not simple accumulation, and it competes with other sinks such as growth and reproduction (Chapin *et al.* 1990). A full understanding of storage of carbohydrate tradeoffs will likely require approaches to separate accumulation from allocation to storage. In this paper, we do not try to separate the two and use the term storage to generally refer to carbohydrates be they accumulated or truly stored.

Important context for understanding carbohydrate storage in xylem is the role storage plays in drought resistance. Species and individuals that have greater stores of carbohydrates have greater drought resistance (Galiano *et al.* 2011; Mitchell *et al.* 2013). Species that differ in the degree to which their tissues dehydrate on a seasonal basis differ in key adaptive traits that place different demands on carbohydrate storage

(Johnson *et al.* 2012). During drought, plants can experience a prolonged reduction in photosynthesis (Martínez-Vilalta *et al.* 2002), where energy reserves support maintenance respiration and defence (McDowell *et al.* 2008; Waring 1987). Moreover, drought may disrupt phloem transport (Sevanto 2014), which may make local storage of carbohydrates all the more important for drought resistance. Species that avoid dehydration have a suite of traits that commonly include stomatal closure, leaf shedding and extensive rooting. All of these traits compromise photosynthesis or, for roots, demand photosynthate for maintenance respiration (Aubrey & Teskey 2009). Species that are tolerant of dehydration may commonly maintain positive photosynthesis when tissues are dehydrated mitigating the need for abundant storage;

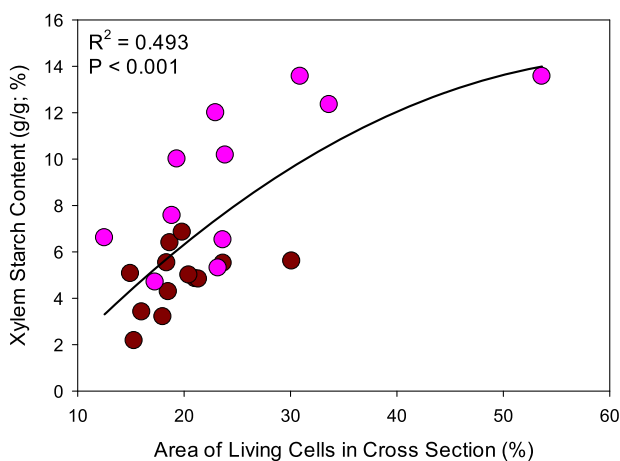


Figure 10. Xylem starch content of branch xylem as a function of the area of living cells in the tissue for temperate tree species (pink dots, Plavcová *et al.* 2016), and chaparral shrubs (red dots, Pratt, unpublished data). The chaparral shrubs include only species that lack living fibres because data were not available for living fibre areas. Starch content for chaparral shrubs was measured in the fall and spring and the highest value was chosen to represent the maximum storage content. Best fit curve and statistics is a logarithmic model and is for all species. Similar methods for starch analysis were used for analysing starch in tissues (see methods in Plavcová *et al.* 2016 and Pratt *et al.* 2014).

however, this hypothesis has received mixed support and is an area of active research (García-Fórner *et al.* 2016; McDowell *et al.* 2008; Skelton *et al.* 2015). Nevertheless, dehydration-tolerant species should have lower respiratory costs associated with a less extensive root system, thus requiring fewer stores for maintenance. Dehydration tolerant species may also convert their stored starch or fructans to simpler sugars in order to osmotically adjust and maintain turgor (Sevanto *et al.* 2014). In summary, we predict that carbohydrate storage is inversely related to dehydration tolerance, and therefore cavitation resistance.

Carbohydrate storage space is in the living cells and should be determined by the volume of living cells in tissue. Woody species widely differ in parenchyma content, and for many species, ray parenchyma are the most abundant living cell type in the xylem with axial parenchyma being more variable (Morris *et al.* 2016; Spicer 2014). This indicates a wide divergence in potential carbohydrate storage. Recent work among trees from a temperate climate and from chaparral shrubs supports the connection between parenchyma and storage capacity in that there is a positive association between parenchyma cell content and carbohydrate storage in branch xylem of angiosperms (Fig. 10; Plavcová *et al.* 2016; Pratt, unpublished data). This was supported when carbohydrate content was expressed as percentage per unit dry mass of tissue and as carbohydrate mass per volume of tissue.

Tradeoffs associated with carbohydrate storage may relate to space packing, that is, if stems and roots are packed with relatively more parenchyma they will then have less volume to fill with fibres and vessels leading to tradeoffs. The increase in parenchyma content (percent area in cross section) of sapwood is negatively associated with fibre content and is independent of vessel content (Fig. 2; Ziemińska *et al.* 2015). Thus, there is a clear basis to link maximum carbohydrate storage to a mechanical tradeoff; however, this needs to be tested. Arrangement of fibres to reinforce vessels or stems is also likely to be important in achieving mechanical stability. For example, abundant paratracheal parenchyma that surround vessels may be an arrangement that destabilizes vessels that could make vessel implosion more likely unless vessel walls are thickened

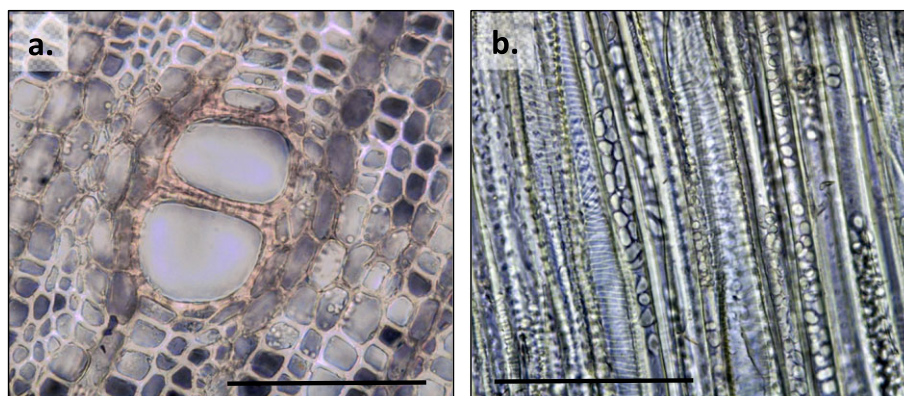


Figure 11. Unstained fresh cross section of branch wood of *Laguncularia racemosa* (white mangrove; a) and longitudinal section of branch from *Arcostaphylos glandulosa* (Eastwood Manzanita; b). The xylem of white mangrove has abundant paratracheal parenchyma and vessels with thick walls. The xylem of this manzanita has many living fibres that contain abundant starch granules. The scale bars in the images are 100 µm.

(Fig. 11a). Short of implosion, the strain associated with tension on water columns may lead to bending of cell walls, pit apertures and pit membranes that could nucleate cavitation (Jacobsen *et al.* 2005).

One factor that could compensate for a weakening of tissue strength because of abundant parenchyma is to employ living fibres for carbohydrate storage in lieu of parenchyma (Carlquist 1988; Carlquist 2014). This would maintain strength and increase storage capacity (Fig. 11b). We have observed abundant living fibres in many chaparral shrubs species that are highly tolerant of dehydration (e.g. some *Arctostaphylos* spp.). We are unaware of any study examining the distribution of living fibres across a broad range of floras. If these tracheids are important in dehydration tolerance, they might be more represented among taxa adapted to semi-arid and arid habitats.

Tradeoffs between xylem storage and cavitation resistance may arise for multiple reasons, and they may also lead to indirect tradeoffs with transport efficiency. We already mentioned that dehydration avoidance and tolerance mechanisms have implications for carbon balance, which leads to a predicted negative relationship between storage and cavitation resistance. This tradeoff is supported for chaparral shrub species (Fig. 12). There are other factors that likely relate to this relationship. For example, if parenchyma do destabilize vessels, this may limit the tensions that can be tolerated in the context of vessel implosion, which is consistent with the pattern found for chaparral shrubs (Fig. 12). Another explanation for this relationship could be that greater carbohydrate storage is important for vessel refilling. It is well documented that starch conversion in xylem parenchyma is associated with the refilling process (Bucci *et al.* 2003; Salleo *et al.* 2004; Secchi & Zwieniecki 2011). Thus, species with refilling capacity might have lower safety and rely on refilling, which is also consistent with an inverse relationship between safety and storage of carbohydrates (Fig. 12). If this were the case, an indirect association may arise corresponding

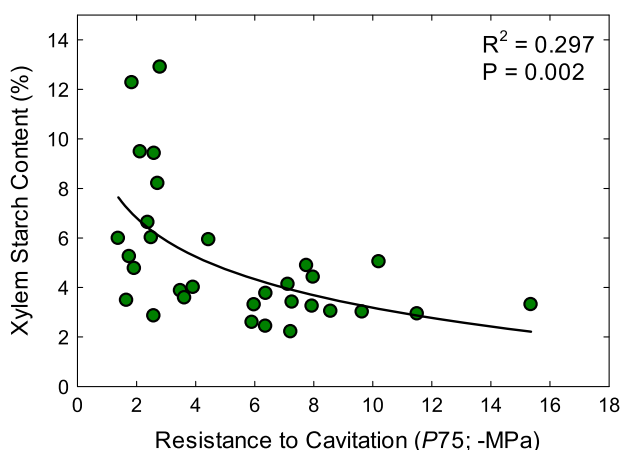


Figure 12. Xylem starch content of woody branch xylem of chaparral shrubs measured in the fall dry season in the mediterranean-type climate region of southern California as a function of the xylem resistance to cavitation (Pratt, unpublished data). Best fit curve and statistics is a logarithmic model.

to a positive relationship between carbohydrate storage and xylem efficiency.

SUMMARY

A previous review of xylem transport and biomechanics summarized xylem function in the context of a ‘tradeoff triangle’ with xylem safety, efficiency and mechanical support occupying the corners of the triangle (Baas *et al.* 2004). We summarize xylem tradeoffs here adding another axis occupied by storage to create a ‘tradeoff diamond’ (Fig. 13). Many of these tradeoffs are well supported while others have yet to be tested and remain open hypotheses.

As storage has not been a chief focus of xylem tradeoff analyses, there is much uncertainty related to this function. Storage of both water and carbohydrates affects the carbon economy of plants; thus, tradeoffs can be expected to arise for both economic and structural reasons chiefly related to fibres and parenchyma and how they interact with vessels. There are many exciting insights to be gained from examining the role of storage in xylem function such as the role of living fibres in storage, mechanics and dehydration tolerance. Recent work has found that individuals with greater carbohydrate stores are more drought resistant (Dickman *et al.* 2014; Mitchell *et al.* 2013). It seems likely that many aspects of storage will indirectly tradeoff with other xylem functions. Because of this, it will be useful to use statistical methods that account for networks of associations such as path analysis and structural equation modelling.

Another area of limited knowledge relates to the xylem structure and function of diverse positions and organs within woody plants. Limited knowledge of how xylem varies within organisms makes scaling to whole organism function difficult. Most data to date have focused on interspecific studies of branch xylem. Expanding data collection to include roots, both young and older, and trunk xylem is a critical area of future research.

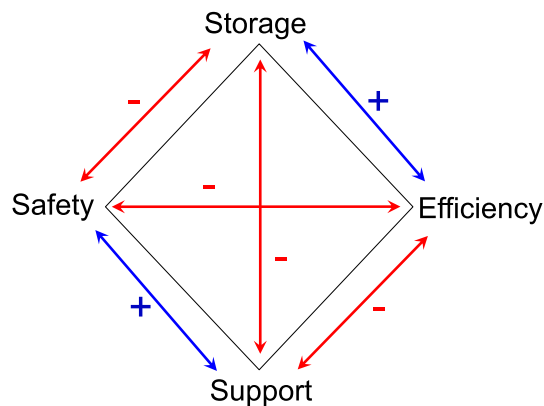


Figure 13. Summary of relationships (tradeoffs) among four xylem functions. Storage in this case refers to both water storage (capacitance) and carbohydrate storage, which give rise to the same set of predictions, but for different reasons in some cases. Red lines denote a negative association between two functions and blue lines a positive one. Some of these relationships arise because of direct factors while other operate indirectly as discussed in the text.

Xylem is one of the most abundant tissues on earth, and its function, production and decomposition have a major impact on regional and global hydrological and carbon cycles (Chave *et al.* 2009). This tissue has been central to the evolution and radiation of the flowering plants that dominate much of the globe. Understanding the diverse structural and functional relationships of xylem helps to elucidate the evolutionary history of plants and predict the future of ecosystems in the context of environmental change. Xylem safety is of keen interest because of its role in drought resistance of plants (Choat *et al.* 2012; Sperry & Love 2015). Along with safety, efficiency and mechanical tradeoffs, storage is a critical function of xylem and is associated with many of the dynamic aspects of xylem function. Its link with drought resistance, along with xylem safety, forms the basis for its use in modelling vegetation response to environmental change (McDowell *et al.* 2013). Further studies of storage tradeoffs should help refine these models, which becomes more pressing in the context of recent tree dieoffs and a warming and drying climate (Allen *et al.* 2015).

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