

Chapter 7

Integrative Xylem Analysis of Chaparral Shrubs

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1 Chaparral Shrublands

1.1 *The Ecological and Evolutionary Context of a Model Community for Physiological Studies*

The chaparral shrub community is dominated by evergreen sclerophyllous shrubs and primarily occurs in southern California (Fig. 7.1a) (Parker et al. [in press](#)). The chaparral has probably been more studied in an ecophysiological context than any other natural vegetation type in the world. The species that dominate this vegetation type have proven to be excellent model organisms for a range of physiological studies including studies of photosynthesis (Field and Mooney 1986), water relations (Morrow and Mooney 1974; Poole and Miller 1975), drought tolerance (Harrison et al. 1971; Kolb and Davis 1994), and xylem structure and function (Carlquist and Hoekman 1985; Hargrave et al. 1994; Wagner et al. 1998). This chapter will focus on xylem traits and for a recent broader review see Parker et al. ([in press](#)).

There are important reasons why chaparral vegetation has drawn the attention of physiologists (reviewed in Field and Davis 1989). One chief reason is that the environment where chaparral occurs is predictably stressful, thus providing a clear ecological context for understanding stress resistance traits. The source of the stress is the Mediterranean-type climate that characterizes the region where chaparral occurs in California. The precipitation falls as rain in the winter months when the temperatures are cool and the summers are hot with a predictable 4–6 months rainless period (Cowling et al. 2005). During the summer and fall, many species develop considerable water deficits and consistently have some of the lowest water potentials ever measured (Oechel 1988; Davis et al. 2002; Jacobsen et al. 2007a, b).

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Fig. 7.1 A typical chaparral shrubland in the winter months in the western Santa Monica Mountains with bright green redshank (*Adenostoma sparsifolium*) and white flowering big-pod ceanothus (*Ceanothus megarcarpus*) in the foreground and background (panel **a**). (**b**) A photograph taken March 2014 of a chaparral shrubland in the Cold Creek of the Santa Monica Mountains suffering under extreme drought stress during the current multiyear drought gripping California. The plants in the photo are mostly evergreens so the lack of green and nongreen colors indicates shrubs that have dieback or that are dead. The green plant in the foreground is on the side of the road and receives extra runoff water and the oaks in the middleground are trees with access to stream water. Photos taken by R. Brandon Pratt

Beyond the summer rainless period, there is wide natural variability in annual rainfall from year to year and decade to decade. These extreme events place considerable stress on shrubs beyond an average year (Jacobsen et al. 2007a, b) and it is not uncommon to observe dieback and mortality of adult shrubs during these droughts (Fig. 7.1b) (Horton and Kraebel 1955). This readily observable stress leads to clear and frequent selection for traits related to drought (Davis et al. 2002; Pratt et al. 2014). Moreover, when droughts happen, they create opportunities for natural experiments to study mechanisms of drought response and survival (Parsons et al. 1981; Davis et al. 2002; Paddock et al. 2013; Pratt et al. 2014), which has also been the case in other Mediterranean-type ecosystems (Peñuelas et al. 2001; Vilagrosa et al. 2003; Lloret et al. 2004).

Field and Davis (1989) describe the “chaparral era” of physiological ecology studies as one typified by integration. One important theme of these studies has been cross-ecosystem comparisons of convergent evolution between chaparral and the four other regions of the world that have a Mediterranean-type climate: the cape region of South Africa, central Chile, Southwest Australia, and the Mediterranean basin (Mooney and Dunn 1970; Jacobsen et al. 2009). A related approach has been to compare chaparral communities to other non-Mediterranean-type shrub communities to examine which traits are unique to Mediterranean-type species (Bhaskar et al. 2007; Jacobsen et al. 2007a, b). Other studies have sought to integrate functional traits over different spatial and temporal scales (Miller and Poole 1979; Miller 1981; Davis and Mooney 1985; Cornwell and Ackerly 2009). These studies have included analyses over evolutionary timescales that have examined the evolutionary impact of the onset of the Mediterranean-type climate as well as the role of ecological sorting processes on functional traits of extant species (Ackerly 2004a, 2009).

1.2 Implications of Mediterranean-Type Climate for Vascular Function

In the context of vascular function, being evergreen means that chaparral shrubs have to maintain hydraulic supply to leaves during the dry season and during drought. This has been a key selective force for xylem resistance to cavitation and some chaparral shrubs are among the most cavitation resistant woody species known (Jacobsen et al. 2007a, b). Co-occurring chaparral shrub species can have rooting depths ranging from shallow to deep leading to a range of functional types arrayed along a drought avoidance to tolerance continuum (Hellmers et al. 1955; Thomas and Davis 1989; Ackerly 2004a, b; Parker et al. *in press*). Minimum seasonal water potential experienced by a species is strongly correlated to resistance of xylem to cavitation (Fig. 7.2). This suggests that xylem cavitation is a key trait that is linked to the level of water deficit experienced by adult shrubs. It has also been shown that seedling mortality during drought is correlated to cavitation resistance, which is another indication that cavitation resistance is an important drought tolerance trait (Fig. 7.3). Xylem refilling is unlikely to be important for chaparral shrubs

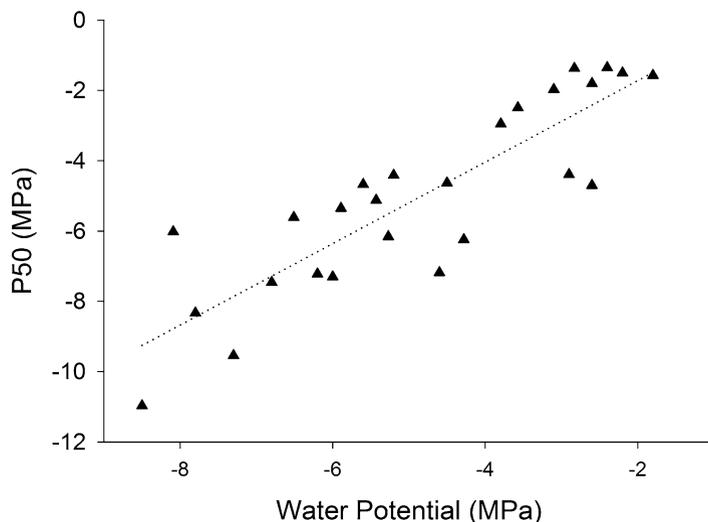


Fig. 7.2 The relationship between the minimum water potential experienced during the dry season and the resistance of branches to xylem cavitation (P50). Cavitation resistance was measured as the point where 50 % of hydraulic conductivity has been lost (P50) relative to the maximum conductivity with emboli removed by a flushing treatment. Data are means of both cavitation resistance and water potential measured at predawn (Jacobsen et al. 2007a, b; Pratt et al. 2007a, b)

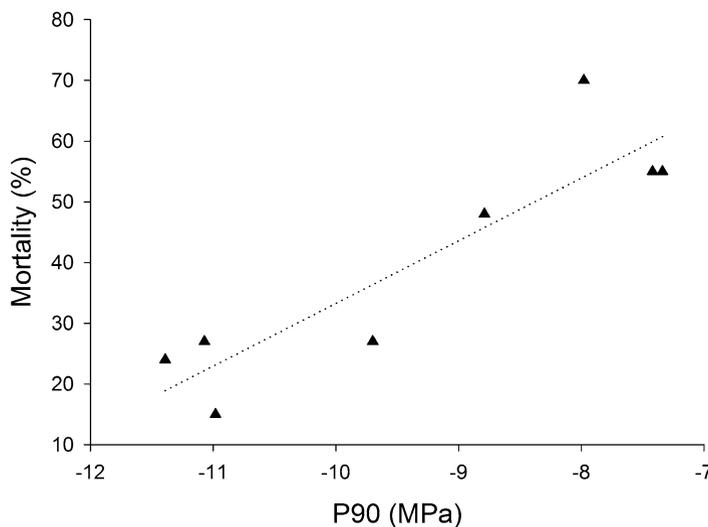


Fig. 7.3 Mortality of anisohydric-type seedlings during drought plotted against cavitation resistance of stems (P90). Figure modified from Pratt et al. (2008)

during the dry season because most shrubs will be beyond the water potential where refilling can occur (Hacke and Sperry 2003); moreover, the protracted rainless season means that plants will stay predictably dry until the fall and winter months when rains come, thus refilling would be futile.

Freeze/thaw stress has also been found to be an important force affecting chaparral shrub physiology and distributions (Ewers et al. 2003; Davis et al. 2005, 2007; Pratt et al. 2005). When the sap in the xylem freezes, air bubbles come out of solution and can expand upon thawing leading to gas-filled or embolized vessels. Species that have larger vessel diameters are more vulnerable to freeze/thaw-induced cavitation (Davis et al. 1999a, b). Freeze/thaw stress can also interact with drought. If the fall/winter rains do not occur before December (often the month with the lowest annual temperature) then the vascular system will be exposed to freeze/thaw stress when the xylem is under significant tension, which has been shown to lead to even greater levels of embolism than freezing in a hydrated state (Langan et al. 1997; Davis et al. 2005, 2007; Pittermann and Sperry 2006). Freeze/thaw stress at colder sites has been a factor limiting the maximum vessel diameter of a species (Ewers et al. 2003), and may have affected xylem structure in other ways such as patterns of vessel grouping (Carlquist 1984), and the presence and abundance of tracheids.

1.3 Integrative Studies of Xylem Traits

There are many scales over which xylem has been studied in chaparral and an exhaustive review of all of them is beyond the scope of this chapter. Some of these studies have been aimed at furthering our understanding of plant vascular function, while others have used xylem traits to test hypotheses about ecology and evolution of chaparral shrubs. Of course these two study aims are not mutually exclusive and many studies shed light on both.

One important theme has been the examination of xylem traits across multiple life stages. The crown fire regime in chaparral means that plants are top-killed by fire, which has a strong influence on community dynamics. Most species either resprout or recruit seedlings from a dormant seed bank after fire, and some species even do both (Keeley et al. 2012). The seedling stage, being small and shallowly rooted, is often the one exposed to the most extreme levels of water deficits and is one of the most vulnerable stages to mortality (Frazer and Davis 1988; Thomas and Davis 1989; Williams et al. 1997; Pratt et al. 2005). Thus, the xylem traits of seedlings are under keen selection to survive the summer dry season and stiff competition for resources in their first year of life. Selection at the seedling stage may determine many important xylem adaptations of a species and, without ontogenetic plasticity or allometric shifts, the xylem traits we measure on adults may be more a reflection of what happens at the seedling stage than conditions experienced at the adult stage (Pratt et al. 2007a, b, 2008).

In addition to seedlings, recent studies have suggested that xylem resistance to cavitation is important for drought survival of postfire resprouting chaparral species (Utsumi et al. 2010; Pratt et al. 2014). Interestingly, resprouts generally have reduced resistance to cavitation compared to unburned adult plants (Ramirez et al. 2012), and the anatomical/mechanistic reasons for this are currently under study (Anna Jacobsen, unpublished manuscript). The different ways that species cope with fire (resprouting vs. seedling recruitment) shift their allocation of resources and lead to trade-offs with implications for their physiological adaptations, including vascular traits (Pratt et al. 2007a, b, 2012a, b). Studies across different life stages will continue to be an important area of research and will help shed light on xylem plasticity across these stages, as well as how selection operates across the whole life cycle (Poorter 2007).

Another area of integration are studies examining xylem traits across multiple organs. This has been done many times comparing branches and roots (Davis et al. 2002; Pratt et al. 2007a, b, 2008); some have compared leaves and stems (Méndez-Alonzo, unpublished manuscript; Pratt, unpublished manuscript); and others have examined leaves, shoots, branches, fine roots, and root systems (Pratt et al. 2010). An important result from these studies is that roots are typically more vulnerable to cavitation than stems; however, because roots have much greater maximum conductivity than stems even when they are highly embolized they can still achieve similar conductivity to stems that are far less embolized (Pratt et al. 2008). Selection operates on intact functioning individuals so studies of the vascular system as an integrated unit are ultimately important to understand vascular adaptations.

Few studies have sought to examine xylem traits across space and time (Anderegg and Meinzer 2015). It has been shown that xylem cavitation resistance can shift over the course of a season (Jacobsen et al. 2007a, b). This shift is not one-directional and some species shift to being more vulnerable, but more commonly species shift to being more resistant during the dry season (Jacobsen et al. 2007a, 2014). Examination of cavitation resistance across moisture gradients has found that chaparral at drier sites has greater resistance to cavitation than those at moister sites (Davis et al. 1999a), whereas for some taxa, e.g., *Arctostaphylos* spp., there seems to be very little change (Vasey et al. 2012; Jacobsen and Pratt 2013).

Studies of trade-offs in xylem function has been an active area of chaparral research. One of the earliest of these studies to examine a trade-off other than between safety and efficiency was the relationship between transport efficiency and mechanical strength (Wagner et al. 1998). Since then, many important studies have expanded the study of mechanical strength and transport traits (Hacke et al. 2001; Jacobsen et al. 2005). Greater mechanical strength of chaparral xylem is generally associated with greater cavitation resistance (Jacobsen et al. 2007a, b). Water storage (capacitance) and carbohydrate storage are also negatively correlated with cavitation resistance (Pratt et al. 2007a, b; Anderegg and Meinzer 2015). The trade-off between xylem safety from cavitation and efficiency in transport is an influential model and forms the basis for new analyses in the following sections of this chapter.

A final area of study has been to compare the xylem of chaparral to the xylem of other woody communities in California and to the fynbos in South Africa. The goals of these studies have been to identify traits unique to the chaparral, which would

indicate that they are important in the context of the stressful Mediterranean-type climate (Carlquist and Hoekman 1985; Carlquist 1989; Hacke et al. 2009). Other studies have addressed the question of convergent evolution of vascular traits to assess if chaparral are more similar to species inhabiting Mediterranean-type climate regions on other continents than species inhabiting regions with non-Mediterranean-type climates (Jacobsen et al. 2009; Pratt et al. 2007a, b). If a trait is found to be convergent in similar environments when compared across distantly related taxa that are separated by large geographical expanses, then this is among the strongest demonstrations that a trait is adaptive in the context of that environment. Key xylem traits such as cavitation resistance, xylem efficiency, and xylem density are convergent among South African and Californian Mediterranean-type shrublands when compared to other semiarid and arid shrublands (Jacobsen et al. 2009).

The remainder of this chapter will integrate long-standing ideas gleaned from comparative xylem studies regarding the importance of various xylem traits for contributing to xylem safety of chaparral shrubs with current models of xylem safety and efficiency.

2 Ecological Xylem Anatomy of Chaparral

Chaparral species were a key part of a seminal ecological xylem anatomy study by Sherwin Carlquist and David Hoekman (Carlquist and Hoekman 1985). This study, and other related ones (Carlquist 1989; Rosell et al. 2007), demonstrated many important trends regarding xylem anatomical traits linked to xylem safety. Many of these discoveries are only recently being fully appreciated among physiologists for their insight and importance for xylem function generally (Lens et al. 2011). At the time Carlquist conducted many of his studies of chaparral xylem there was not a database of xylem safety and efficiency measures that could be used to test some of his ideas. This is no longer the case and there is an extensive database of these traits for chaparral shrubs (Jacobsen et al. 2007a, b; Pratt et al. 2007a, b; Hacke et al. 2009). In the following sections, and in the spirit of the “integrative era” of chaparral studies, we review some of Carlquist’s findings and, where possible, integrate these data with published and unpublished data on xylem safety and efficiency to independently and directly test some of Carlquist’s hypotheses about chaparral xylem safety.

There are many xylem anatomical features of chaparral shrub xylem that reflect the water stress regime that these angiosperms experience. One feature is the presence of tracheids and their role in safe transport of water. Carlquist and Hoekman (1985) distinguish between three types of tracheids: true tracheids, vascular tracheids, and vasicentric tracheids. True tracheids are ancestral and along with parenchyma make up the background tissue of the xylem. Vascular and vasicentric tracheids are found among species in lineages that lost tracheids through the evolution of fiber-tracheids and libriform fibers. Thus, in these species tracheids were reevolved and represent a derived character. Vascular tracheids are located at the end of a growth ring and are hypothesized to be a safe transport pathway to keep the cambium hydrated, especially in drought-deciduous species. Being evergreen, these

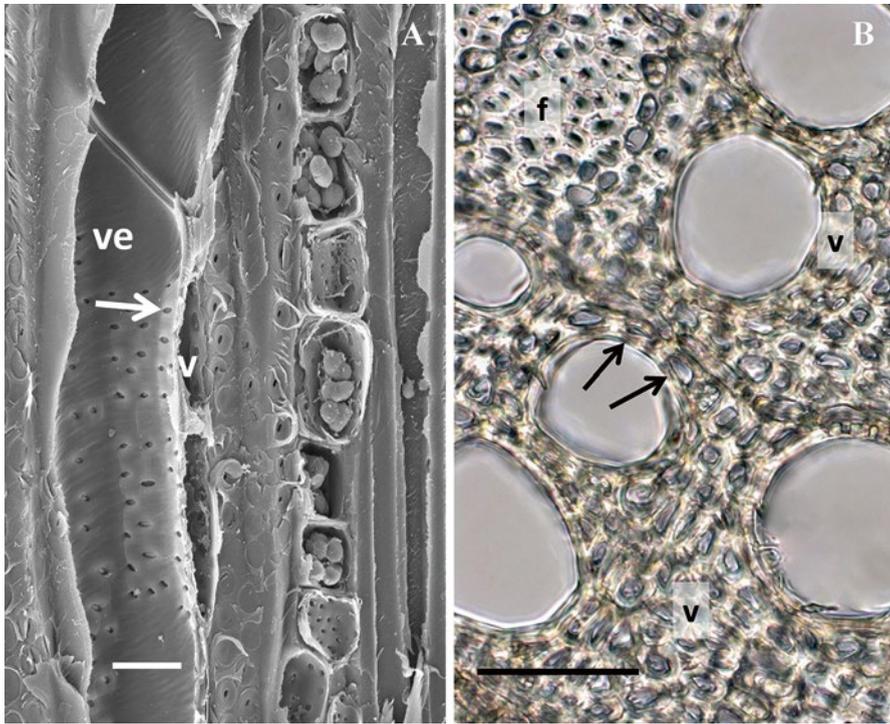


Fig. 7.4 (a) Scanning electron micrograph of xylem of big-pod ceanothus (*Ceanothus megacarpus*). Of note is the imperforate vascentric tracheid (v) that shares a wall with the vessel element (ve) left of center, and this wall has numerous large circular bordered pits indicating the role of transporting water for the tracheids (arrow). Scale bar is 20 μm . Micrograph taken by Anna L. Jacobsen. (b) A light micrograph ($\times 400$ magnification) showing the abundant vascentric (v) tracheids that surround the large vessels in scrub oak (*Quercus berberidifolia*). Also seen are libriform fibers (f) and large pits between vascentric tracheids and vessels (arrows). The scale bar is about 42 μm . Micrograph was taken by Marta Percolla

tracheids are not common among chaparral shrubs and will not be emphasized in this review (Carlquist 1989). Vascentric tracheids are located around vessels and these are hypothesized to aid in transport safety for many chaparral shrubs (Fig. 7.4a, b). These tracheids are hypothesized to form a water filled sheath around vessels that minimize air-filled compartments from which air might seed. The different tracheid types are generally mutually exclusive and the presence of true tracheids precludes the presence of vascentric or vascular tracheids (Carlquist 1989).

To determine the importance of these tracheids, Carlquist compared the prevalence of the different types of imperforate tracheary elements among chaparral species to the prevalence in other California plant communities (Carlquist 1989). Among chaparral species, 43.9 % have vascentric tracheids and among species that lacked true tracheids and vascular tracheids (i.e., those species that could potentially have vascentric tracheids), 75 % had vascentric tracheids. By contrast, compared to a sample of species taken across a range of environments from within California,

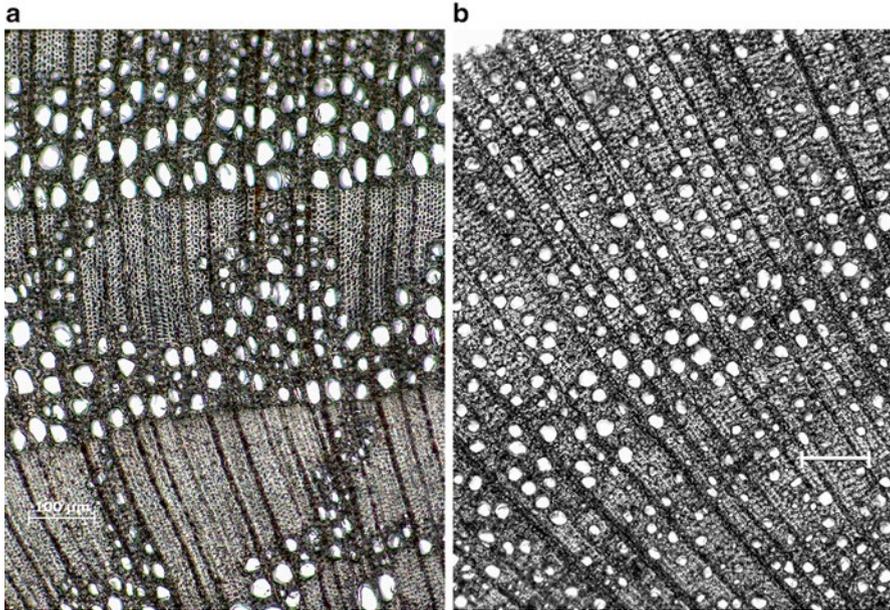


Fig. 7.5 (a) Light micrograph showing grouped vessels surrounded by vascentric tracheids in cup leaf ceanothus (*Ceanothus greggi* var. *vestitus*) and (b) the generally solitary and nongrouped vessels generally surrounded by true tracheids of toyon (*Heteromeles arbutifolia*). Both images are $\times 100$ and the scale bars are $100\ \mu\text{m}$. Micrographs taken by Brandon Pratt

these same numbers are lower at 33.3 % and 52.3 %, respectively. Among riparian species, none have vascentric or vascular tracheids (Carlquist 1989).

The importance of vascentric tracheids is that they maintain connections between vessels that are separated by an embolized vessel. This maintains the vessel network under times of drought. Tracheids have narrow diameters and are not able to transport water as efficiently as vessels, but during the dry season water use is greatly restricted, so the inefficient tracheids may be sufficient to supply transpiration. Similar to vascentric tracheids, the presence of true tracheids is hypothesized to maintain the vessel network, which precludes a need for vascentric and vascular tracheids.

Tracheid presence has been hypothesized to affect vessel grouping among chaparral species and species more generally (Carlquist 1989, 2009; Rosell et al. 2007). The presence of nonconductive imperforate tracheary elements (fiber-tracheids and libriform fibers) in the background xylem tissue is associated with greater groupings of vessels (Fig. 7.5). On the other hand, the presence of abundant true tracheids in the background tissue may minimize vessel grouping (Fig. 7.5) (Rosell et al. 2007). The reasons for these patterns were studied by Carlquist (1984) who hypothesized that the benefit of vessel groups is to increase connections among conduits because if one vessel embolizes then it is connected to other vessels in the network. In other words, in species lacking the network connections afforded by true tracheids, vessel groups lead to a safer vascular system in the context of cavitation. Angiosperm tracheids of any type may be safer than vessels because they are

more abundant and they may be more resistant to cavitation (Hargrave et al. 1994). Species with vasicentric tracheids that only have tracheids around their vessels have to form vessel groups to take advantage of the connections offered by the tracheids (Fig. 7.5), but they show wide variation in this trait (Rosell et al. 2007), which may be related to the abundance of vasicentric tracheids they have.

2.1 Imperforate Tracheary Element Type and Safety: A Test of Carlquist’s Hypothesis

When examined using published data, and consistent with Carlquist’s hypotheses, chaparral species that had libriform fibers were least resistant to cavitation (Fig. 7.6a). The next least resistant group were those species with vascular tracheids, which were all drought-deciduous species. Deciduous chaparral shrubs are generally more vulnerable to cavitation than evergreens (Parker et al. in press), thus tracheid type and leaf habit are confounded for this group; moreover, this analysis is

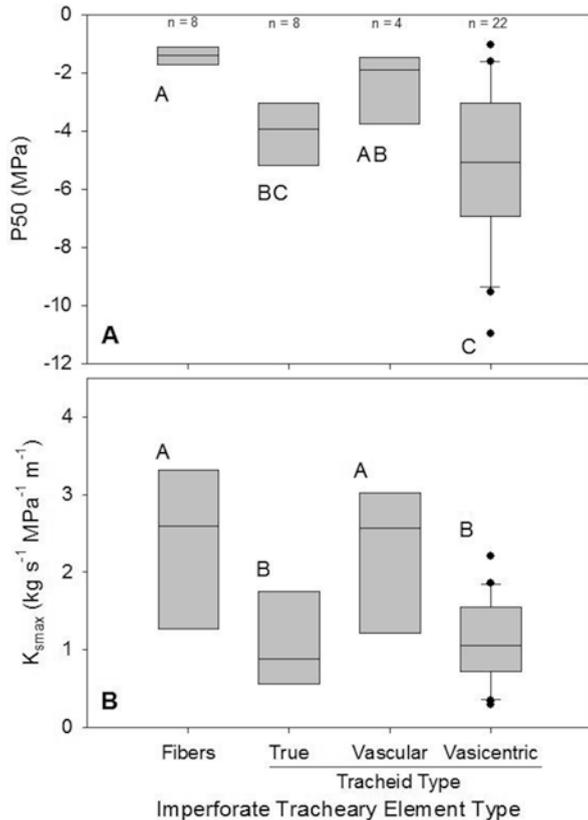


Fig. 7.6 (a) Box plots plotted for cavitation resistance (P50) and (b) xylem specific conductivity, i.e., efficiency (K_{smax}) plotted for species that differ in the background imperforate tracheary element type. For the box plots the middle line represents the median and lower and upper lines of the box represent the 25th and 75th percentiles, respectively. The error bars (whiskers) are the 5th and 95th percentiles and data points shown are outliers that are beyond that. Error bars are only calculated for a sample size of 9 or greater. Boxes with unique letters are significantly different (1-way ANOVA on log transformed data)

limited by sample size (data are available for only four species containing vascular tracheids) (Fig. 7.6a). Species with true tracheids had relatively safe xylem compared to the other groups (Fig. 7.6a). Species with vascentric tracheids had the most resistant xylem; although, they were also the most variable group indicating that the presence of vascentric tracheids does not necessarily lead to high levels of safety (Fig. 7.6a). A trade-off between safety and efficiency may explain why species with vascentric tracheids do not uniformly have highly safe xylem.

These data are broadly supportive of Carlquist's hypotheses about the importance of tracheids in conferring xylem safety to drought. A key challenge remains to understand the mechanism of how tracheids contribute to xylem safety during drought (Hargrave et al. 1994). The tracheids may lead to greater safety because there are so many of them that they create redundancy (Ewers et al. 2007) or the pit and pit membrane characteristics of these tracheids may be modified for safety (Jansen et al. 2009; Plavcová et al. 2013). The small diameter of tracheids precludes rapid uptake of dye tracers and they are not generally resolvable with *en planta* imaging techniques, thus significant challenges remain in the study of these tracheids.

2.2 Trade-off Between Safety and Efficiency: The Role of Tracheids

Xylem safety generally comes at a cost of xylem efficiency and this may also relate to imperforate tracheary element type. The species that had true and vascentric tracheids had the least efficient xylem compared to species with libriform fibers and vascular tracheids. These patterns point to a trade-off between safety and efficiency that may be linked to tracheid type (Figs. 7.6b and 7.7). It is possible that the trade-off between safety and efficiency is related to having tracheids with narrow lumens that are not efficient (Tyree and Ewers 1991) and this limits the maximum efficiency for species with tracheids. Alternatively, species with tracheids may be those that inhabit the driest sites and thus have reduced efficiency for evolutionary/ecological reasons, not simply because they have tracheids.

The rare pit hypothesis (a.k.a the pit area hypothesis) is currently an important framework for understanding the trade-off between xylem safety and efficiency (Hargrave et al. 1994; Wheeler et al. 2005; Christman et al. 2009). According to this hypothesis, species that have greater pit area or pit numbers for a vessel have a greater chance of having a large pore in a pit membrane that is vulnerable to cavitation by air-seeding (Lens et al. 2011). The pit area hypothesis has been examined in southern California shrubs (Hacke et al. 2009), but chaparral shrubs have not been separately analyzed. A plot of pit area/vessel area against cavitation resistance appears to show a strong relationship between these two traits that is consistent with the rare pit hypothesis; however, there is one extreme outlier that defies the overall trend (Fig. 7.8).

The outlier in this analysis, *Quercus beberidifolia*, has low pit area and low resistance to cavitation. This combination of traits should lead to high safety and low

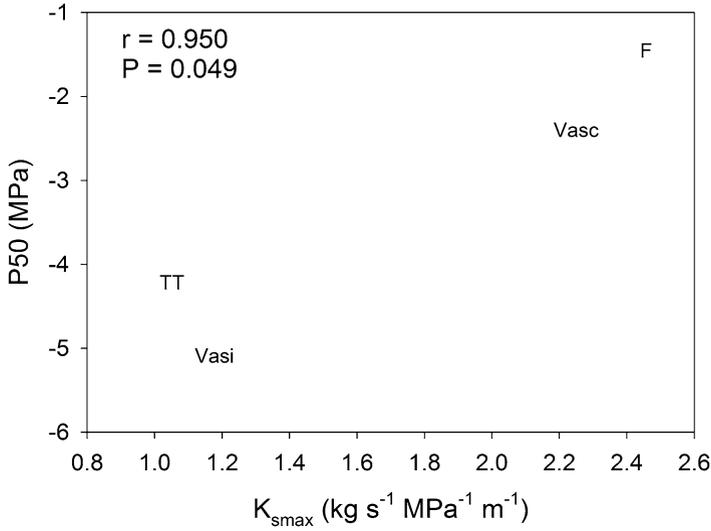


Fig. 7.7 Cavitation resistance (P50) plotted against xylem efficiency (K_{smax}) illustrating a trade-off between safety and efficiency for species with different imperforate tracheary element types: true tracheids (TT), vasicentric tracheids (Vasi), vascular tracheids (Vasc), and libriform fibers (F)

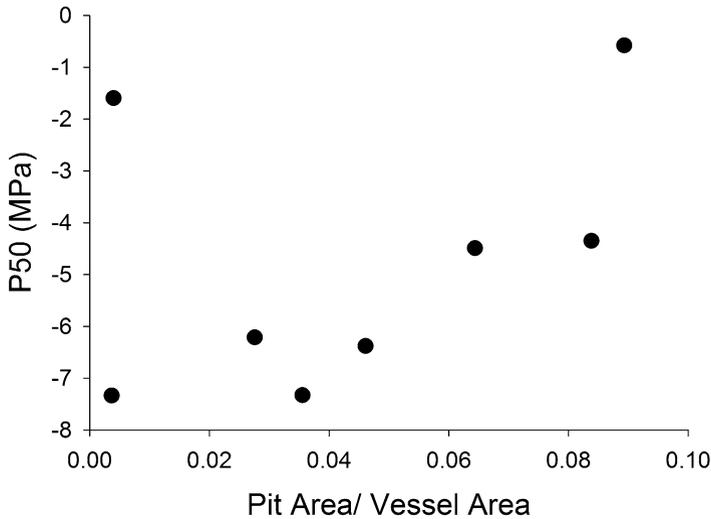


Fig. 7.8 The relationship between cavitation resistance (P50) and intervessel pit area/vessel area. The outlier in the upper left part of the figure is *Q. berberidifolia*

efficiency, but just the opposite is observed and this species has relatively high efficiency and low safety. The main xylem structural feature that leads to this species having low pit area is that it has many solitary vessels and thus a low proportion of vessel wall area in contact with adjacent vessels (Fig. 7.4b). Solitary vessels are common to *Quercus* spp. (Wheeler and Thomas 1981; Carlquist 1984). This anatomy is made possible because of abundant vasicentric tracheids (Fig. 7.4b). Interestingly, *Q. berberidifolia* has relatively high K_s compared to other chaparral species (only 7 species have higher values out of 47 species in the database). Thus, these tracheids can apparently achieve high levels of transport efficiency, and one reason they can do so is because they are highly abundant (Carlquist and Hoekman 1985; Rosell et al. 2007). It is also possible that they have modified pit and pit membrane traits such as membrane thickness, pit pore aperture, or pit membrane area that contribute to their efficiency (Hacke and Jansen 2009; Jansen et al. 2009; Lens et al. 2011). *Quercus crispula* was documented to have large pores in the pit membranes of its vasicentric tracheids, which could increase efficiency and decrease safety (Sano and Jansen 2006). Whatever modifications have been made they have compromised safety, as these oaks are vulnerable to water stress-induced cavitation when compared to other chaparral species (Jacobsen et al. 2007a, b; Tobin et al. 2013). These considerations highlight an unappreciated role that anatomical constraints may play in the trade-off between safety and efficiency and offer an explanation of why oak species may be generally vulnerable to cavitation (Tobin et al. 2013; Martin-StPaul et al. 2014). It would be valuable in future studies to examine pit area between vessels and tracheids on *Quercus* spp. in the context of the rare pit hypothesis, and such an analysis should lead to *Q. berberidifolia* falling farther to the right on the x -axis in Fig. 7.8.

The narrow diameters of the tracheids should render them resistant to freeze/thaw stress (Davis et al. 1999a, b; Pittermann and Sperry 2003). This suite of xylem anatomical traits may be linked to the evolutionary history of oak species. These species have an arcto-tertiary biogeographical origin whereby they colonized the warmer and milder regions of California from more northern regions (Axelrod 1983; Manos and Stanford 2001). Tracheids are an asset for safety in areas of freeze/thaw stress (Chap. 3), which would have been common in the regions occupied by ancestral *Quercus* spp., and also characterizes many of the habitats that oaks presently occupy.

2.3 Integrating Vessel Grouping with Current Models of Vessel Connectivity

The connections between vessels as part of the xylem network have been the topic of recent studies (Schenk et al. 2008; Martínez-Vilalta et al. 2012). Vessel connectivity (defined here as the number of unique vessels a vessel shares a wall with) has been hypothesized to be associated with safety and efficiency, with greater connectivity being associated with greater efficiency (xylem specific conductivity) and lower safety (Loepfe et al. 2007). This is hypothesized to be the case because greater

connectivity increases the pathways for air to spread among vessels once one becomes embolized. It also creates more pathways for water to move radially, thus increasing overall efficiency. Carlquist's ideas of vessel grouping are partially at odds with the connectivity hypothesis of Loepfe et al. (2007). He suggested that greater vessel grouping is associated with greater safety because if one vessel embolized then connections to other vessels can maintain continuity of the pathway (Carlquist 1984). However, the type of imperforate tracheary elements present are important in Carlquist's conception of the hypothesis, and vessel grouping only becomes important for safety in species with libriform fibers or vasicentric tracheids in the background tissue. It is important to note that species with vasicentric tracheids surrounding vessels may tend to form vessel groups, but they could still have low connectivity with respect to vessel-to-vessel connections (e.g., *Ceanothus greggi* var. *vestitus* Fig. 7.5). If tracheids are safer, i.e., more cavitation resistant (this will certainly be the case for freeze/thaw stress), then vessels that are grouped could be safe if they have abundant vessel-to-tracheid connectivity, but not vessel-to-vessel connectivity (Carlquist 2001).

Vessel connectivity was examined in the context of imperforate tracheary element type. As expected, connectivity was greatest in species with nonconductive fibers and vascular tracheids in the background tissue (Fig. 7.9). Species with true

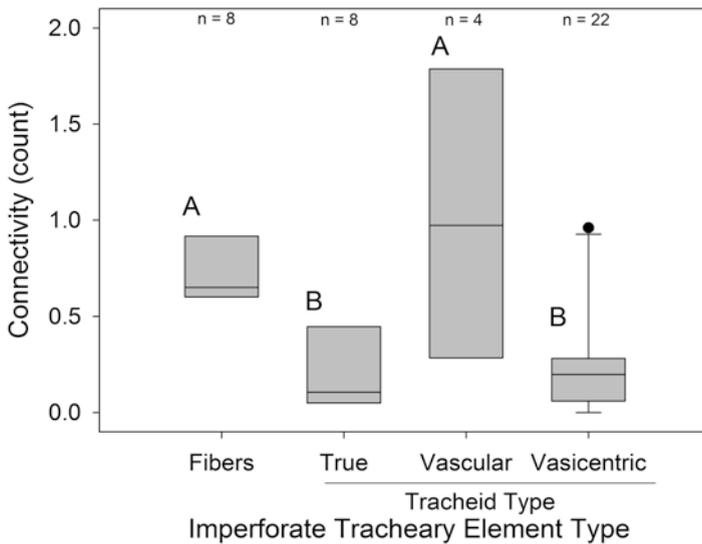


Fig. 7.9 Box plots plotted for connectivity (the number of unique vessels a vessel shares a wall with) plotted for species that differ in the background imperforate tracheary element type (Percolla and Pratt, unpublished data). For the box plots the middle line represents the median and lower and upper lines of the box represent the 25th and 75th percentiles, respectively. The error bars (whiskers) are the 5th and 95th percentiles and data points shown are outliers that are beyond that. Error bars are only calculated for a sample size of 9 or greater. Boxes with unique letters are significantly different (1-way ANOVA on log transformed data)

tracheids and vasicentric tracheids were not significantly different. These results suggest that estimates of connectivity are linked to the type of imperforate tracheary element in the background tissue of xylem and the presence of true or vasicentric tracheids limits connectivity. We did not have enough data on vessel grouping to do a robust analysis of the relationship between vessel grouping and connectivity, but preliminarily the association is not significant. This is not surprising because species with vasicentric tracheids can have high numbers of vessels per group and have low levels of connectivity. Mean connectivity for the different imperforate tracheary element groups was strongly and positively correlated to xylem efficiency (compare Fig. 7.6b and 7.9; $r=0.917$, $P=0.083$), which supports the hypothesis of Loepfe et al. (2007).

A recent study examined the relationship between connectivity and cavitation resistance in *Acer* spp. (Lens et al. 2011). *Acer* wood lacks conductive tracheids, thus greater vessel-to-vessel connectivity should confer safety according to Carlquist's hypothesis and should be more vulnerable according to Loepfe et al. (2007). Lens et al. (2011) found support for Carlquist's hypothesis and more connectivity was associated with greater cavitation resistance.

3 Conclusions

The xylem of chaparral species will continue to be a model system for ecological xylem anatomy. A fertile area of research will be the continued effort to integrate concepts developed from ecological xylem anatomy studies with current models of xylem function (Lens et al. 2011). For example, it is clear from consideration of *Q. berberidifolia* that tracheids, especially vasicentric ones, are going to have to be integrated into analyses examining pit area and pit numbers in the context of a trade-off between safety and efficiency (Hacke et al. 2009). Moreover, to fully understand the role of vessel connectivity, much more will need to be learned about tracheids and their role in connectivity and sectoriality (Schenk et al. 2008; Martínez-Vilalta et al. 2012). Other areas that are interesting fronts for further work are the helical thickenings on the inside of vessel elements that are associated with xylem safety (Carlquist 1989; Lens et al. 2011). The mechanistic importance of this trait remains unknown. The pit characteristics of chaparral shrubs have not been extensively studied and will likely yield valuable information regarding drought tolerance traits (Jarbeau et al. 1995). Trade-offs in xylem function, be they safety vs. efficiency, safety and biomechanics, or trade-offs with storage continue to be a fruitful area of research (Jacobsen et al. 2005; Pratt et al. 2007a, b; Anderegg and Meinzer 2015).

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