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Title

Low vulnerability to xylem embolism in leaves and stems of North American oaks

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Short title:

Low xylem vulnerability in *Quercus*

One-sentence summary

North American oaks are more resistant to xylem embolism than previously thought, suggesting that avoiding stem embolism is a critical component of drought tolerance in woody trees.

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Author contributions

R.P.S., D.D.A., S.E.T., and T.E.D. contributed to the original research plans, conceived the project, and designed the experiments; R.P.S. and A.P.W. performed most of the experiments; R.P.S., D.D.A., Y.S., and A.P.W. analysed the data; R.P.S. wrote the article with contributions of D.D.A., S.E.T., T.E.D., and A.P.W.

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Abstract

Although recent findings suggest that xylem embolism represents a significant, drought-induced damaging process in land plants, substantial debate surrounds the capacity of long-vesselled, ring-porous species to resist embolism. We investigated whether recent methodological developments could help resolve this controversy within *Quercus*, a long-vesselled, ring-porous temperate angiosperm genus, and shed further light on the importance of xylem vulnerability to embolism as an indicator of drought tolerance. We used the optical technique to quantify leaf and stem xylem vulnerability to embolism of eight *Quercus* species from the Mediterranean-type climate region of California, USA, to examine absolute measures of resistance to embolism as well as any potential hydraulic segmentation between tissue types. We demonstrated that our optical assessment reflected flow impairment for a subset of our sample species by quantifying changes in leaf hydraulic conductance in dehydrating branches. Air-entry water potential varied twofold in leaves, ranging from −1.70 ± 0.25 MPa to −3.74 ± 0.23 MPa, and fourfold in stems, ranging from −1.17 ± 0.04 MPa to −4.91 ± 0.30 MPa. Embolism occurred earlier in leaves than in stems in only one out of eight sample species, and plants always lost turgor before experiencing stem embolism. Our results show that long-vesselled North American *Quercus* species are more resistant to embolism than previously thought, and support the hypothesis that avoiding stem embolism is a critical component of drought tolerance in woody trees. Accurately quantifying xylem vulnerability to embolism is essential for understanding species distributions along aridity gradients and predicting plant mortality during drought.

Introduction

Drought can cause major damage to plant communities (Adams et al., 2010) and reduce plant primary productivity. Although species-specific damage thresholds are not yet fully understood (Anderegg et al., 2012), recent findings indicate that post-drought recovery of gas exchange in conifer and angiosperm plant species can be predicted by properties of the water transport system (Brodribb and Cochard, 2009; Anderegg et al., 2015; Skelton et al., 2017b). Under drought stress, the continuous column of water in the plant xylem experiences increasing tension caused by declining water potential at the sites of evaporation (usually in the leaf mesophyll). Eventually, air is drawn into the water transport system, forming embolism in the xylem conduits (Sperry and Ikeda, 1997). Although plants have developed several mechanisms to restore vessel functionality by refilling embolised vessels (Brodersen et al., 2010), those that have experienced a loss of hydraulic conductance due to embolism formation within the xylem do not always recover full hydraulic functionality following rehydration and often suffer reduced gas exchange capacity as a result (Skelton et al., 2017b). Plants often die when water potentials drop below those associated with extensive hydraulic dysfunction (>50 % loss of hydraulic conductance in conifers and >88% in angiosperms) (Brodribb and Cochard, 2009; Choat, 2013; Urli et al., 2013; Brodribb et al., 2014).

Consequently, the capacity of plants to resist embolism formation in the xylem is hypothesized to be a major component of plant drought tolerance and survival. This is consistent with several observations: (i) *in situ*, species tend to maintain positive safety margins between plant water potential and water potential values that induce extensive embolism in stems (Choat et al., 2012) and (ii) the capacity of xylem to withstand water deficit is significantly correlated to the aridity of the environment that species tend to inhabit for many taxa (Brodribb and Hill, 1999; Pockman and Sperry, 2000; Maherali et al., 2004; Choat et al., 2012; Blackman et al., 2014; Larter et al., 2017), but not all (Brodribb et al., 2014). Imperfect correlations between xylem resistance to embolism and aridity in these taxa may arise in part due to plants relying on additional traits or behaviours to convey drought tolerance or to avoid exposure to drought, such as low minimum leaf conductance, deep-rooting or drought-induced leaf shedding (Ackerly, 2004; Brodribb and Holbrook, 2004; West et al., 2012; Brodribb et al., 2014; Maréchaux et al., 2015; Hochberg et al., 2017).

Stomatal closure before embolism formation has been theoretically advanced as another fundamental component of plant drought tolerance (Jones and Sutherland, 1991; Sperry et al., 2002; Delzon and Cochard, 2014; Martin-StPaul et al., 2017). Early stomatal closure serves to reduce water loss and maintain a positive safety margin between plant water potential and water potential inducing embolism, thus allowing plants to avoid water-deficit–induced damage, except under severe drought conditions (Hochberg et al., 2017; Skelton et al., 2017a; Skelton et al., 2017b; Charrier et al., 2018). Current empirical datasets indicate that most, but not all, plants tend to exhibit conservative, positive safety margins (Brodribb and Holbrook, 2003; Choat et al., 2012; Skelton et al., 2015), supporting the hypothesis that stomata have evolved to close before water potential-induced embolism. However, relatively few studies have explicitly investigated the precise timing of stomatal closure in relation to the point of xylem embolism formation (Hochberg et al., 2017; Skelton et al., 2017a), and it is necessary to address this fundamental aspect of plant physiology.

Thus, although xylem resistance to embolism and early stomatal closure during periods of water deficit appear to be important properties of drought tolerance in land plants, fundamental questions about these properties remain unresolved. Critically, the xylem vulnerability to embolism of many plant taxa remains unmeasured or uncertain because of methodological difficulties of studying xylem under tension, or potential methodological artefacts related to specific techniques for assessing xylem vulnerability to embolism (Melcher et al., 2012; Sperry et al., 2012; Cochard et al., 2013; Wheeler et al., 2013;

Rockwell et al., 2014). Of particular concern are long-vesselled angiosperm species (including many tropical trees, temperate ring-porous trees, and woody vines), as these species are thought to be prone to an ‘open-vessel’ artefact, potentially resulting in spuriously low resistance to embolism. Several studies have suggested that xylem of some plant species might be highly vulnerable to embolism, having produced so-called ‘r’ shaped xylem vulnerability to embolism curves (i.e. exponential curves, rather than the more commonly observed sigmoidal curves) (Jacobsen et al., 2007b; Sperry et al., 2012). Yet, many of the species thought to be highly vulnerable to embolism occur in semi-arid or water-stressed environments, frequently experience low water potentials, and, if these values are correct, would thus either be experiencing regular damage or regular xylem refilling to maintain hydraulic function (Bucci et al., 2003; Jacobsen et al., 2007a; Jacobsen et al., 2007b; Nardini et al., 2008; Johnson et al., 2009; Johnson et al., 2011; Ogasa et al., 2013; Trifilò et al., 2015).

In addition, to better understand the capacity of a single species to withstand embolism, it is important to examine points of hydraulic failure within distinct plant tissues (Zimmermann, 1978; Tyree and Ewers, 1991), since different tissues can vary in their capacity to withstand xylem embolism (Tyree et al., 1993; Johnson et al., 2011). The so-called ‘vulnerability segmentation’ between tissues possibly serves to create hydraulic fuses within the plant to further protect the more valuable tissues from drought damage. This hypothesis is consistent with observations that more distal tissues in woody trees, particularly leaves of drought-deciduous species, are often more vulnerable to water deficit than stems or large branches (Cochard et al., 1992; Tyree et al., 1993; Choat et al., 2005; Johnson et al., 2011; Hochberg et al., 2017), and with a lack of segmentation shown in evergreen herbaceous species that proportion biomass relatively evenly among tissues (Skelton et al., 2017a). However, few studies have explored variation in the degree of segmentation between tissues among closely related species; consequently, the factors contributing to inter-specific variation in segmentation remain unclear.

Recent advancements in visual or optical techniques for quantifying xylem vulnerability to embolism offer potential to investigate embolism formation within different species and among distinct tissues to address current uncertainties and controversies in xylem physiology in plants (Brodribb et al., 2016b; Brodribb et al., 2017; Skelton et al., 2017a). Here, we investigated patterns in leaf and stem xylem vulnerability to embolism in *Quercus* (oaks), a diverse, long-vesselled (Jacobsen et al., 2007b; Hacke et al., 2009; Jacobsen et al., 2012), ring-porous temperate angiosperm genus, with species distributions spanning aridity gradients in western North America. Our main objectives were to examine: (1) how the capacity to withstand embolism within leaves and stems varies across *Quercus* species; (2) whether any segmentation between leaves and stems occurs within species; and (3) whether vulnerability to embolism in leaves and stems is a critical component of drought tolerance in this ecologically important genus. We hypothesized that embolism avoidance in stems is a critical component of drought tolerance in these long-lived woody tree species and thus made four main predictions: (i) stems will display low vulnerability to embolism; (ii) leaves will embolise earlier than stems in response to water deficit; (iii) stomatal closure will occur before embolism in stems of all species; (iv) species occurring in more arid environments will display greater resistance to embolism in stems than those restricted to more mesic environments. To test these predictions, we selected eight deciduous and evergreen *Quercus* species with varying climatic niches from the Mediterranean-type climate region of California (USA) and quantified leaf and stem xylem vulnerability to embolism using newly developed optical techniques. For a subset of our species, we also quantified leaf hydraulic conductance in response to water deficit, to demonstrate that our optical curves reflect changes in xylem capacity to transport water. Finally, we quantified the turgor loss point (TLP) of five sample species, to gain a proxy for stomatal closure.

Results

Variation in leaf and stem xylem vulnerability to embolism among Quercus *species*

We observed considerable inter-specific variation in the leaf and stem water potentials associated with embolism in our sample of eight *Quercus* species (Fig. 1; Fig. 2; Table 1). We used the leaf or stem vulnerability curves to quantify a standardised metric to compare species (i.e. P_e, water potential at initialization of embolism), and found that the eight sample *Quercus* species varied twofold in leaf vulnerability (Fig. 3a; Table 1; $F = 11.39$; d.f. = 7; $p = 1.76 \times 10^{-5}$) and fourfold in stem xylem vulnerability to embolism (Fig. 3b; Table 1; $F = 6.89$; d.f. = 7; $p = 0.00564$). The species most vulnerable to xylem embolism was *Quercus sadleriana* (Leaf $P_e = -1.78 \pm 0.08$ MPa; Stem $P_e = -1.17 \pm 0.04$ MPa), while *Q. berberidifolia* (Leaf $P_e = -3.74 \pm 0.23$ MPa; Stem $P_e = -4.26 \pm 0.31$ MPa) and *Q. douglasii* (Leaf $P_e = -3.13 \pm 0.26$ MPa; Stem $P_e = -4.91 \pm 0.30$ MPa) were the least vulnerable to embolism (Fig. 3; Table 1).

We observed low vulnerability to embolism in both cut and intact individuals of *Q. wislizenii* (Fig. 4). Leaves of the potted, intact individuals were slightly less vulnerable to embolism ($P_e = -3.71$ MPa) than leaves of the cut branches ($P_e = -2.89 \pm 0.22$ MPa; Fig. 4). Stems of the potted, intact individuals ($P_e = -3.71$ MPa) were highly consistent with stems from the cut branches (-3.56 ± 0.19 MPa; Fig. 4).

Although we observed substantial inter-specific variation in the magnitude of the water potentials associated with embolism in leaves and stems, the shape of the vulnerability curves was similar for all species. Specifically, in each of our eight sample species, the progression of total cumulative embolism in the xylem of leaves and stems when plotted against leaf or stem water potential approximately followed a sigmoidal pattern (Fig. 2). The shape of the vulnerability curves observed in intact, potted individuals of *Quercus wislizenii* was also sigmoid and highly consistent with our observations of cut branches from field-grown plants of the same species (Fig. 4).

Vulnerability segmentation in Quercus *species*

Our data show that leaf xylem was as vulnerable to embolism as stem xylem in all species, except *Q. sadleriana* and *Q. douglasii* (Fig. 2 insets). Leaves were more vulnerable than stems in *Q. douglasii* ($\Psi_{leaf} - \Psi_{stem}$ = 1.6 MPa; t = −4.46, d.f. = 3.89, p = 0.01), while the reverse was observed in *Q. sadleriana* ($\Psi_{leaf} - \Psi_{stem}$ = −0.61 MPa; t = 6.52, d.f. = 2.87, p = 0.008).

Relationship between turgor loss and xylem vulnerability to embolism

The safety margin between the water potential associated with turgor loss and that associated with the onset of embolism within leaves (i.e. TLP – Ψ_e, in MPa) tended to be very small in all species (Fig. 5). Safety margins ranged from + 0.38 MPa in *Q. agrifolia* (i.e. turgor loss before embolism) to −0.11 MPa in *Q. kelloggii* (Fig. 5). Safety margins between turgor loss and the onset of xylem embolism within stems were much greater and tended to increase with greater resistance to embolism formation (Fig. 5). In stems, safety margins ranged from +1.76 MPa in *Q. douglasii* to +0.29 MPa in *Q. garryana* (Fig. 5).

Relationship between vulnerability to embolism and aridity

The *Quercus* species from the western United States occupy regions with different levels of climatic water deficit (Fig. 6), indicating that they occupy distinct climatic niches related to water availability. Species climatic niches range from that of *Q. sadleriana* (A), restricted to mesic sites (climatic water deficit [CWD] < 600 mm), to that of *Q. berberidifolia* (G), inhabiting xeric sites in California. We found a significant positive correlation between the aridity of the sites that individuals tend to occupy and the resistance to embolism of both leaves (Fig. 6a) and stems (Fig. 6b). *Q. sadleriana* and *Q. garryana,* the two species with the least resistant xylem, are restricted to sites that are much more mesic than *Q. berberidifolia*, the species with the most resistant xylem (Fig. 6).

Discussion

Our study applies the optical method of quantifying xylem embolism resistance to investigate fundamental physiological and ecological questions associated with xylem embolism in plants. Specifically, our observations of variation in resistance to embolism within leaves and stems in *Quercus* species, in combination with observations of points of turgor loss, leaf habit and climatic niches, allow us to draw several important conclusions about the aspects of drought tolerance within this ecologically important genus. Firstly, our observations of the capacity of western North American *Quercus* species to resist embolism within leaves and stems indicate that *Quercus* species may be considerably more resistant to water deficit than previously thought (see Jacobsen et al., 2007a; Jacobsen et al., 2007b; Sperry et al., 2012). Secondly, our finding that leaves were at least as resistant to embolism as stems in seven out of eight species indicates that leaves do not serve as hydraulic fuses in this genus, contrary to the segmentation hypothesis. Thirdly, that turgor loss occurs either at or before the point of incipient embolism in leaves and stems supports the prediction that stomata will close earlier than the onset of xylem embolism during periods of water deficit (Martin-StPaul et al., 2017). Finally, the clear positive association between the aridity of the sites that a species occupies and the capacity to withstand embolism supports the notion that xylem resistance to embolism is an important component of drought tolerance.

High resistance of Quercus *species to embolism*

Substantial debate currently surrounds the capacity of long-vesselled, ring-porous temperate plants to resist embolism. The finding that all eight of our sample *Quercus* species have P_{50} values below −2 MPa suggests that trees and shrubs in this ecologically important genus might be more resistant to embolism than previously thought. This conclusion is at odds with several previous results showing stems in some *Quercus* species to be highly vulnerable (Jacobsen et al., 2007c; Sperry et al., 2012). However, our findings are consistent with a recent assessment of xylem vulnerability to embolism in European oaks showing that species from this genus are highly resistant to embolism (Lobo et al., 2018). Our findings also agree with several recent studies that have similarly suggested that other long-vesselled, woody species are more resistant to embolism than previously reported, including grapevine (Choat et al., 2010; Hochberg et al., 2017; Charrier et al., 2018) and olive (Rodriguez-dominguez et al., 2018). It has previously been suggested that vulnerability curves generated on short branch segments (<30 cm) of long-vesselled plants using the centrifuge technique might suffer from an open-vessel artefact (Sperry et al., 2012; Cochard et al., 2013) and might underestimate vulnerability to embolism (Choat et al., 2010). Our findings provide important support for this claim in an ecologically diverse and often ecologically dominant North American genus.

In addition, the finding that all sample *Quercus* species displayed sigmoid-shaped curves contrasts previous reports of exponential or ‘r-shaped’ curves in this genus (Jacobsen et al., 2007c; Sperry et al., 2012). In particular, our observation that *Quercus wislizenii* stems display sigmoidal vulnerability curves is at odds with previously published reports of r-shaped curves in this species (Jacobsen et al., 2007c). Notably, the previously published r-shaped curves were generated from relatively short branches using the centrifuge technique. Here, we were able to validate our observations of sigmoid vulnerability curves obtained from cut branches of *Quercus wislizenii* by observing embolism formation in intact trees of this species (Fig. 4), confirming our result. This important finding suggests that r-shaped curves in other *Quercus* species are likely to be a product of an ‘open-vessel’ artefact associated with the centrifuge technique and should be revisited.

Lack of vulnerability segmentation in Quercus *species*

Our study reports evidence of a lack of vulnerability segmentation in six out of eight sample North American *Quercus* species. Differences between the mean water potential associated with embolism formation in leaves and those in stems were statistically significant in only two cases (*Q. douglasii* and *Q. sadleriana*, and the latter had more vulnerable stems than leaves). These results are consistent with previous findings for European *Quercus* species (Cochard et al., 1992) and suggest that when segmentation between leaves and stems exists, it might often be slight. Thus, our finding that the mean water potential associated with embolism formation in leaves was similar to that in stems contradicts the hydraulic fuse hypothesis (that leaves will embolise before stems to protect the more valuable tissues).

Although there was no clear general relationship between leaf habit and segmentation, leaf shedding during severe drought events may play a substantial role in avoiding stem embolism in certain *Quercus* species. We note that *Quercus douglasii*, the species with the greatest degree of segmentation between leaves and stems and a species most resistant to xylem embolism, is also considered to be one of the only drought-deciduous oak species in California (i.e. it drops its leaves during periods of severe water deficit) (Griffin, 1973). Recently, leaf shedding has also been found to be associated with leaf embolism and avoidance of extensive stem embolism in other drought-deciduous woody plant species (Hochberg et al., 2017), indicating that this process might be an important additional component of drought tolerance. Future studies should investigate the complexity of leaf habit, further exploring differences between drought-deciduous and winter-deciduous leaf habits in drought-prone habitats.

Xylem vulnerability and stomatal closure in Quercus *species*

In a subset of the species studied, we observed that the point of bulk leaf turgor loss occurs very close to or before incipient embolism in the leaf and consistently before incipient embolism within stems, further enhancing support for the hypothesis that avoidance of embolism within stems is a critical component of drought tolerance in *Quercus*. This finding is consistent with those of other studies on different plant genera showing that stomatal closure pre-empts xylem embolism (Brodribb et al., 2003; Trifilò et al., 2014; Martin-StPaul et al., 2017; Li et al., 2018), and suggests that early stomatal closure might be a widespread strategy to prevent embolism formation that has evolved within land plants.

Our finding that safety margins between TLP and P_e in leaves are small is somewhat surprising, since a recent study found that the water potentials associated with stomatal closure and incipient embolism were similar for only a small number of species, with most species closing their stomata far before embolism (Martin-StPaul et al., 2017). However, our findings are consistent with a study that found strong 1:1 correspondence between the water potential at stomatal closure and incipient embolism formation across twelve ecologically diverse species from temperate Australian woodlands (Li et al., 2018). If avoiding water potentials associated with embolism is important to long-lived oaks, then close co-ordination between stomatal closure and P_e suggests that minimum stomatal conductance is low in these species. Although this hypothesis has been demonstrated to be true in conifer species (Brodribb et al. 2014), it has yet to be tested in angiosperms. Our results also indicate that safety margins between TLP and P_e were larger in stems than leaves, and increased with greater resistance to embolism. This finding provides further evidence that avoiding embolism in stems is critical to avoiding drought-induced damage in oaks.

Although it has been suggested that some plants rely on osmotic adjustment during a season to maintain water uptake and cell turgor (Chaves et al., 2009; Blum, 2017), the close association between P_e in leaves and TLP observed at the beginning of the season in *Quercus* leaves indicates that osmotic adjustment during a season is likely to be relatively small in these species. These findings are consistent with a previous suggestion that a lack of osmotic adjustment might be inherent in certain North American *Quercus* species (Abrams, 1990).

Xylem vulnerability to embolism and drought tolerance

Low xylem vulnerability to embolism in both stems and leaves of Californian *Quercus* species is associated with increasing aridity of the sites that species are able to occupy, providing additional support for our hypothesis that xylem vulnerability to embolism is a key component of drought tolerance in *Quercus*. This hypothesis is further supported by historical observations of minimum seasonal water potentials in two Californian *Quercus* species (*Q. douglasii* and *Q. agrifolia*) during severely dry years, which closely match our P_e values for these species. Midday leaf water potential values have fallen as low as −4.8 MPa for individuals of *Q. douglasii* (stem $P_e = -4.91 \pm 0.3$ MPa) and −2.9 MPa for individuals of *Q. agrifolia* (stem $P_e = -3.56 \pm 0.19$ MPa) (Griffin, 1973; Osuna et al., 2015). Both studies noted little or no drought damage in individuals of these species during the severely dry periods, findings that are consistent with the hypothesis that water potentials associated with embolism in stems represent critical thresholds of drought-induced damage.

Plant functional traits that vary systematically across environmental gradients are considered adaptive because they enhance species performance and survival under particular environmental conditions (Ackerly, 2003). Our study provides evidence that vulnerability to embolism of western North American *Quercus* species is an adaptive trait, strongly linked to site aridity and the capacity to withstand drought. This conclusion is highly consistent with previous studies on other plant genera that show that interspecific variation in leaf resistance to embolism influences species distributions across water availability gradients at local scales (Nardini et al., 2012), broad climatic scales (Blackman et al., 2014), and at the dry end of species geographical ranges (Blackman et al., 2012).

Conclusions

Our findings that xylem embolism in *Quercus* occurs at low water potentials, primarily after turgor loss, and that species-specific vulnerability to embolism decreases with increasing aridity of sites that species occupy indicate that the capacity to resist xylem embolism is a key component of drought tolerance within western North American *Quercus* species. Ultimately our data provide additional support for the framework of drought tolerance among land plants that suggests that (1) stomatal closure occurs before embolism and (2) that embolism avoidance, particularly in stems, is a critical component of drought tolerance. It also suggests that previous observations of r-shaped curves in *Quercus* species and other long vessel angiosperms should be revisited (Maherali et al., 2004; Cavender-Bares et al., 2005; Jacobsen et al., 2007a; Jacobsen et al., 2007b; Choat et al., 2012; Sperry et al., 2012; Trifilò et al., 2015). Resolving these concerns will be important for answering fundamental questions about the adaptive capacity of xylem embolism resistance across land plant groups, the importance of dynamic processes of xylem conduit refilling, the ubiquity of early stomatal closure (Skelton et al., 2015), and the influence of xylem vulnerability on species distributions and community composition.

Finally, in instances where plant functional traits have a known mechanistic relationship with specific environmental stresses, such as drought or climatic water deficit, these traits offer insight into how specific changes in the environment might affect future species distributions and vegetation structure and function. Previous studies within western North America have indicated that changes in CWD associated with global climate change might play an important role in determining shifts in plant communities (McIntyre et al., 2015). Although these studies have suggested that *Quercus* species might be less negatively affected by changes in CWD than other tree species in the region, our data suggest instead that *Quercus* species might be closely adapted to specific CWD conditions and therefore potentially highly sensitive to increases in CWD. Combining observations of *in situ* minimum plant water potential with site-specific estimates of aridity (such as CWD) to estimate a safety margin from incipient embolism will be useful for predicting the drought conditions that may cause damage and for predicting the sensitivity of plant communities to potential future changes in climate.

Methods and materials

Sampling strategy and study species

Eight species of *Quercus* (Fagaceae), an ecologically dominant genus in western North America known to have long vessels, as shown by analyses of several species (Zimmermann and Jeje, 1981; Jacobsen et al., 2007b; Hacke et al., 2009; Jacobsen et al., 2012), were sampled. Species were chosen to capture variation in leaf habit (deciduous and evergreen), taxonomic groups, and distributional ranges along the west coast of North America (to capture potential variation in climatic niches). Our study species were all long-lived woody tree or shrub species that grow to between 2 and ~35 m in height. Specifically, we selected four evergreen species and four deciduous species: *Quercus agrifolia* Nee (section: Erythrobalanus, or red oaks) is a widespread, evergreen tree species; *Q. berberidifolia* Liebm. (section: Lepidobalanus, or white oaks) is a large, evergreen woody shrub or small tree found in chaparral or coastal sage scrub communities; *Q. wislizenii* A. DC. (section: Erythrobalanus) is a large, evergreen tree; *Q. sadleriana* R. Br. Campst. (section: Quercus) is a medium-sized evergreen understorey shrub found in coniferous forests in northern California and south-western Oregon; *Q. garryana* Hook. (section: Lepidobalanus) is a deciduous woody tree species occurring in California and Oregon; *Q. douglasii* Hook. & Arn. (section: Lepidobalanus) is a deciduous woody tree species endemic to California; *Q. kelloggii* Newb. (section: Erythrobalanus) is a deciduous woody tree species and *Q. lobata* (section: Lepidobalanus) is a large deciduous, over-storey, woody tree species. Our primary study site, Pepperwood Preserve in Sonoma County, has seven co-occurring *Quercus* species and is located on the west coast of California (38° 34′ 59.64″ N, 122° 44′ 21.81″ W, 441 m elevation). Vegetation at the site is currently predominantly mixed evergreen and deciduous woodland, which occupies vast tracts of California. *Q. sadleriana* has a more limited distribution in high-rainfall regions of northern California and was sampled at the Six Rivers National Forest, Humboldt County, CA, USA. *Q. wislizenii* was sampled from Hopland Research and Extension Center and the Sierra Foothills Research and Extension Center.

Vulnerability to embolism

Large branches of at least six different individuals of each species were collected at predawn from healthy-looking individuals in the field. To avoid any potential artefact associated with open vessels, we ensured that the cut branches were longer than the species’ maximum recorded vessel length (Supplemental Table 1). Where we were unable to determine maximum vessel length for a species (*Q. sadleriana*), we ensured that the branches were cut from the base of the root collar. Upon excision, branches were immediately placed in at least two plastic bags with damp paper towels to prevent further water loss and transported back to the laboratory at the University of California, Berkeley, for processing. There, we used an optical method to capture embolism in both leaves and branches using flatbed scanners in a dark, temperature-controlled room. For each species, at least three branches from different individuals were used to capture embolism events within the leaves according to the methods described by Brodribb et al. (2016b), and at least three branches from different individuals were used to capture embolism events within small branches (<0.5 cm in diameter) according to the methods described by Brodribb et al. (2017). Full details, including an overview of the technique, image processing, as well as scripts to guide image capture and analysis, are available at http://www.opensourceov.org. Extensive validation of the techniques can be found in several recent publications (Brodribb et al., 2016a; Brodribb et al., 2016b; Brodribb et al., 2017; Skelton et al., 2017a; Skelton et al., 2017b). Briefly, for leaves, we secured a healthy, intact leaf between two microscope slides on a flatbed scanner (Epson perfection V800 or V850 Scanner; Epson America) using duct tape. We scanned each leaf in transmission mode (as opposed to reflective mode, to allow light to pass through the leaf xylem) at least once every four minutes for a period of a few days (usually <4 days). For stems, we carefully removed a small section of bark to expose the xylem, placed it face down on the scanner and secured it in place using duct tape. Stems were scanned in reflective mode, which allowed us to observe embolism within the outer few layers of xylem in each stem. Using branches of small sizes for observation reduced, but did not entirely exclude, the possibility that our method might have missed significant radial variation in embolism within branches (i.e. between rings).

As branches were being scanned for leaf or stem embolism, we simultaneously monitored stem and leaf xylem water potential of each individual to measure the level of hydration of each branch. For stem xylem water potential, we placed a stem psychrometer (ICT International, Armidale, Australia) on a large branch neighbouring each scanned branch at more than 60 cm from the cut end of the main branch. Stem psychrometers were connected to the xylem, sealed with high-vacuum grease (Dow Corning Corp., Midland, MI, USA), and secured with Parafilm (Bemis NA, Neenah, WI, USA) to prevent moisture loss. Stem xylem water potential was recorded every 10 min for the duration of the scanning process. We verified the accuracy of the stem psychrometer readings for each branch by periodically measuring leaf xylem water potential using a Scholander-type pressure chamber (PMS Instruments, Corvallis, Oregon, USA) (Fig. S1). For leaf xylem water potential, we excised at least two leaves neighbouring the scanned leaves, immediately wrapped them in moist paper towel and aluminium foil and placed them in plastic bags to prevent further water loss. We measured leaf xylem water potential of each leaf using the Scholander-type pressure chamber. Since branches were largely equilibrated because of being kept in the dark, variation among neighbouring leaves was slight (always <0.1 MPa).

Upon completion, image sequences were analysed to identify embolism events, seen as changes in the reflection of the stem xylem or changes in the transmission of light through the leaf xylem. Image subtraction of subsequent images conducted in ImageJ (National Institutes of Health, Bethesda, MD, USA) was used to reveal rapid changes in light transmission or contrast produced by each embolism event. Slow movements of the stems or leaves caused by drying could easily be distinguished from embolism events and were filtered from the analysis. Embolism events were thresholded, allowing automated counting of each event using the analyse-stack function in ImageJ.

From the thresholded stack of embolism events, we could extract a time-resolved count of embolism events (using the time stamp of each image). We then converted the raw embolism counts to a percentage of total pixels embolised, producing a dataset of time-resolved percent embolism. The time-resolved percent embolism data were combined with the water potential timeline to estimate the leaf or stem xylem water potential associated with each embolism event. Vulnerability to embolism was recorded as the relationship between percent embolism and water potential. We extracted the air-entry water potential (P_e, MPa), defined as the leaf or stem xylem water potential associated with >5 % embolism for each branch. From these data, we calculated a mean P_e ± s.e. for leaves and stems of each species. Several other metrics of xylem vulnerability to embolism have been used extensively in the literature, such as the water potential associated with 50% loss of hydraulic conductance (P_{50}, MPa). P_e was used to identify a critical threshold of embolism. Previous studies have suggested that the point of air-entry (i.e. P_e) represents a point of incipient damage to plant functionality (Skelton et al., 2017b). For consistency with other studies, we also report P_{50} values (Table 1).

Reliability of the optical vulnerability curves

We conducted two experiments to demonstrate that our optical vulnerability curves reliably capture the capacity of plants to withstand embolism. In the first experiment, we aimed to determine, for a subset of our eight sample species, whether observed embolism accurately quantifies changes in hydraulic conductance. To achieve this, we quantified leaf hydraulic conductance in response to water deficit by using the rehydration kinetics method (Skelton et al., 2017b) on cut branches of two sample species, *Q. kelloggii* (deciduous) and *Q. agrifolia* (evergreen). Briefly, for each species, we collected three additional branches from different individuals and dried them on the benchtop. Periodically, we quantified k_{leaf} and water potential (using the methods described in Skelton et al., 2017b) to obtain a complete vulnerability curve for each individual. We then compared the response of k_{leaf} to the percent embolism obtained using the optical vulnerability technique. In both species, percent embolism measured using the optical technique was associated with loss of leaf hydraulic conductance (Fig. S2). In both species, k_{leaf} also remained relatively constant over an initial range of leaf water potentials but declined upon further dehydration (Fig. S2).

Uncompromised water transport followed by rapid decline in hydraulic functional capacity corroborates our observations of an initial lack of embolism, followed by rapid accumulation of embolism events (Fig. S2).

The aim of our second experiment was to demonstrate that our observations of embolism in cut branches accurately reflect total embolism in intact samples, since the vulnerability curves constructed with the optical method might be influenced by the minimum pressure to which the samples have previously been exposed or by an artefact associated with cutting branches. In particular, we wanted to exclude the possibility that our cut branches had already experienced embolism because of prior water stress or cutting. To do so, we quantified embolism in leaves and stems of healthy, well-watered, intact *Quercus wislizenii* individuals that we obtained from a plant nursery. We followed the same protocol outlined earlier to capture embolism formation within newly and fully expanded leaves and stems of intact, hydrated individuals. We were careful to observe the minimum water potential that our potted individuals experienced before being set up on the scanner. Since the minimum water potentials that our potted *Q. wislizenii* individuals had experienced (−0.68 MPa) was well above the point of incipient embolism in leaves (−3.71 MPa) and stems (−3.78 MPa), we were able to exclude the possibility of prior stress causing embolism in these tissues. We report the results from this second experiment in the results section.

Each time branches were collected for optical curves, the *in situ* midday water potential of leaves from the same individuals for each of our study species was also sampled. These data indicate that water potentials experienced by the trees in the field before sampling remained well above those associated with embolism for all species (Supplemental Table 1).

Pressure-volume curves and turgor loss point

To determine a proxy for the point of stomatal closure, we measured the water potential corresponding to bulk leaf turgor loss (TLP, MPa). Previous studies have shown that stomatal aperture is significantly reduced at leaf turgor loss point (Brodribb et al., 2003; Buckley et al., 2003). The point of bulk leaf cell turgor was determined for individuals of five sample species by the relationship between Ψ_{leaf} and water content in the leaf. Branches from well-hydrated individuals of each sample species were cut under water and allowed to hydrate to >-0.1 MPa. From these branches, at least three leaves per species were removed and used to quantify leaf pressure-volume curves using the bench-drying technique (Tyree and Hammel, 1972). The Ψ_{leaf} values and leaf weight were measured periodically until Ψ_{leaf} stopped declining or desiccation-induced cell damage was observed in leaves. At this stage, leaves were placed in a drying oven for at least two days for complete desiccation to determine dry weight. For each leaf, relative water content was determined and plotted against Ψ_{leaf}, and the Ψ_{leaf} at turgor loss was determined as the point of inflection between the linear and non-linear portions of the plot. A mean TLP ± s.e. ($n = 3$) was calculated for each species.

Climatic niche

To determine the aridity associated with the climatic niche of each species, we quantified the CWD (in millimetres) (Flint et al., 2013) associated with all recorded observations of *Quercus* individuals within the Calflora database (Baldwin et al., 2017). For each observation (i.e. coordinate), we calculated mean monthly CWD between 1981 and 2010 using a state-wide basin characterisation model (Flint et al., 2013). We subsequently determined the driest 25th percentile of the 30-year average CWD values for each species and used this measure as a proxy for the aridity that each species experienced in its home range.

Statistical analysis and fit

The relationship between cumulative percent embolism and leaf water potential was fit according to a sigmoid function:

$$\text{Percent embolism} = 100 - 100/(1 + e^{a(\Psi - b)})$$

where ‘a’ corresponds to the sensitivity to decreasing Ψ, and ‘b’ is the Ψ associated with 50% embolism (i.e. P_{50}).

To test for differences in P_e and P_{50} between species, ANOVA, in addition to a post-hoc Tukey HSD test, was used. To evaluate differences between the P_e of leaves and P_e of stems for each species, we used t-tests on each sample species.

Supplemental Data

Supplemental Figure 1: Relationship between leaf water potential and stem water potential.

Supplemental Figure 2: Relationship between leaf hydraulic conductance and observed xylem embolism.

Supplemental Table 1: Maximum vessel length and observed minimum midday water potential of sample species**.**

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Table

Table 1: Comparison of mean P_e and P_{50} values for leaves (n = 3) and stems (n = 3) of our eight sample *Quercus* species.

Species	**Tissue**	**Trait (MPa; mean ± s.e.; n = 3)**	
		P_e	**P_{50}**
Quercus sadleriana	Leaf	**−1.78 ± 0.08**	**− 2.72 ± 0.25**
	Stem	**−1.17 ± 0.04**	**− 2.74 ± 0.20**
Q. garryana	Leaf	**− 1.70 ± 0.25**	**− 2.81 ± 0.27**
	Stem	**− 1.99 ± 0.35**	**− 3.32 ± 0.56**
Q. kelloggii	Leaf	**− 2.47 ± 0.18**	**− 3.62 ± 0.13**
	Stem	**− 3.28 ± 0.58**	**− 4.73 ± 0.64**
Q. lobata	Leaf	**− 2.4 ± 0.24**	**− 3.02 ± 0.18**
	Stem	**− 2.8 ± 0.40**	**− 3.58 ± 0.25**
Q. wislizenii	Leaf	**− 3.10 ± 0.29**	**− 3.77 ± 0.13**
	Stem	**− 3.35 ± 0.31**	**− 4.10 ± 0.24**
Q. agrifolia	Leaf	**− 2.89 ± 0.22**	**− 4.47 ± 0.31**
	Stem	**− 3.56 ± 0.19**	**− 4.32 ± 0.26**
Q. douglasii	Leaf	**− 3.13 ± 0.26**	**− 4.45 ± 0.24**
	Stem	**− 4.91 ± 0.3**	**− 6.27 ± 0.06**
Q. berberidifolia	Leaf	**− 3.74 ± 0.23**	**− 5.52 ± 0.62**
	Stem	**− 4.24 ± 0.18**	**− 5.95 ± 0.38**

Figure legends

Figure 1: Embolism events in the xylem of a *Quercus sadleriana* leaf (A) and stem (C) and a *Quercus berberidifolia* leaf (B) and stem (D) as observed using the optical vulnerability technique. Scale bars indicate the water potential recorded at each event and are different for each figure panel. *Quercus sadleriana* was the least resistant to embolism, and *Quercus berberidifolia* was the most resistant to embolism.

Figure 2: Optical vulnerability curves for leaves (blue) and stems (brown) of all eight sample *Quercus* species: *Q. sadleriana* (A, the least resistant to embolism); *Q. wislizenii* (B); *Q. agrifolia* (C); *Q. berberidifolia* (D); *Q. garryana* (E); *Q. lobata* (F); *Q. kelloggii* (G); and *Q. douglasii* (H). Solid dark lines and the shading indicates the mean observed embolism ± s.e. for each tissue type (n = 3). Light lines indicate raw curves for each individual. The insets in each panel are boxplots showing the mean P_e for leaves and stems for each species. Asterisks indicate species in which the values for leaves and stems were significantly different.

Figure 3: Inter-specific comparisons of the air-entry water potential (P_e; mean ± s.e.; n = 3) for leaves (A) and stems (B). Letters below each boxplot indicate significant differences between species.

Figure 4: A comparison of vulnerability curves generated on cut leaves and branches and a leaf and branch of a fully intact, healthy, well-watered *Quercus wislizenii* individual that had experienced no prior water stress.

Figure 5: A comparison of turgor loss point (TLP, mean ± s.e., n = 3) and air-entry water potential (P_e) of leaves (mean ± s.e., n = 3, blue) and stems (mean ± s.e., n = 3, brown) of five sample *Quercus* species, indicated that TLP was reached at higher water potential values than P_e of leaves and stems of most species.

Figure 6: Climatic water deficit (a proxy for aridity of a site, mm) of the driest 25th percentile of the distribution of eight sample *Quercus* species is significantly associated with the air-entry water potential (P_e, mean ± s.e., n = 3) of both leaves (A) and stems (B). Species with lower resistance to embolism occur in much more mesic sites than those with greater resistance to embolism.

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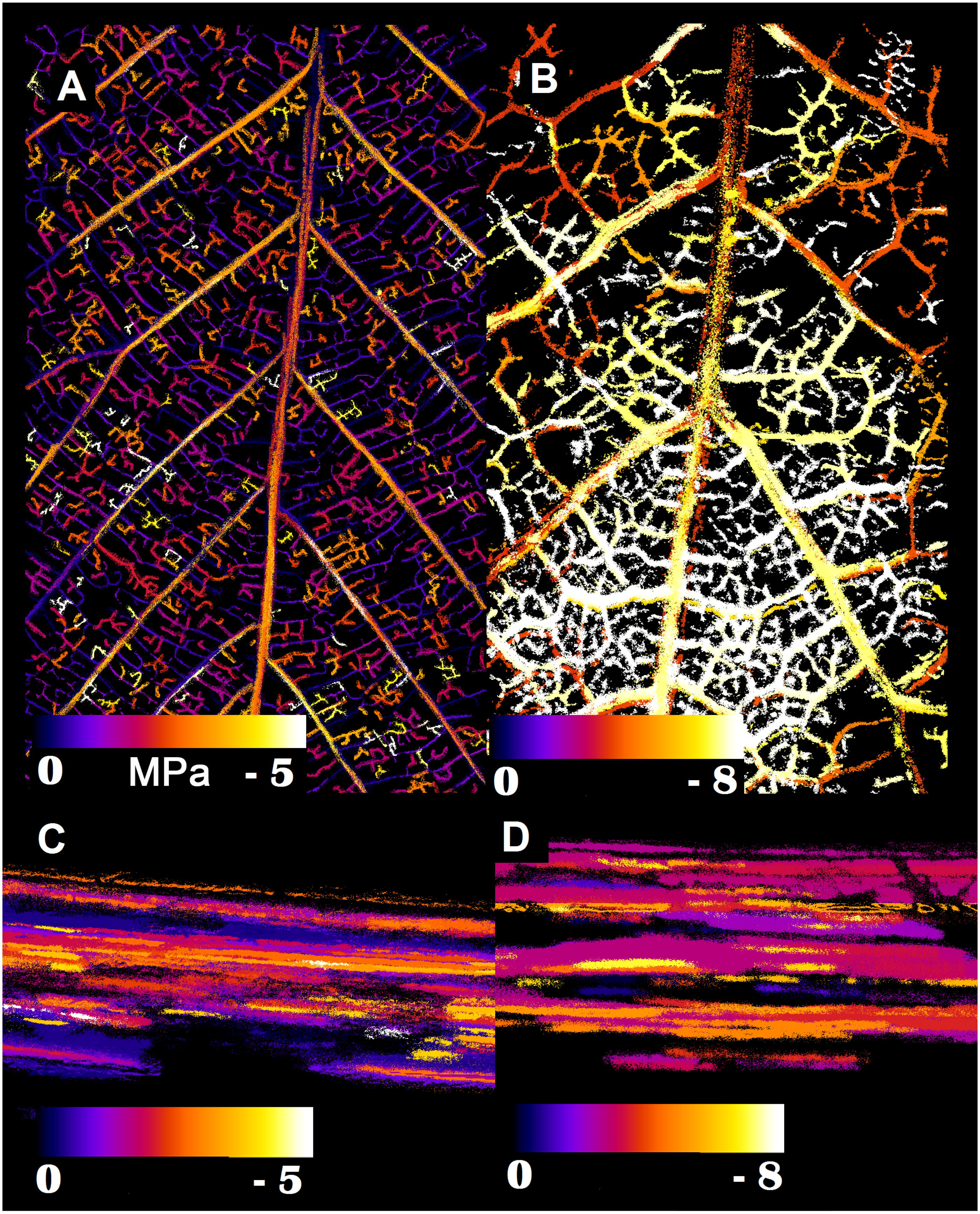

Figure 1: Cumulative observations of embolism events in the xylem of a *Quercus sadleriana* leaf (A) and stem (C), and a *Quercus berberidifolia* leaf (B) and stem (D) captured using the optical vulnerability technique. Scale bars in each panel indicate the water potential recorded at each event (note that scale bars are different for each species). *Quercus sadleriana* was least resistant to embolism among our seven sample species, and *Quercus berberidifolia* was the most resistant to embolism.

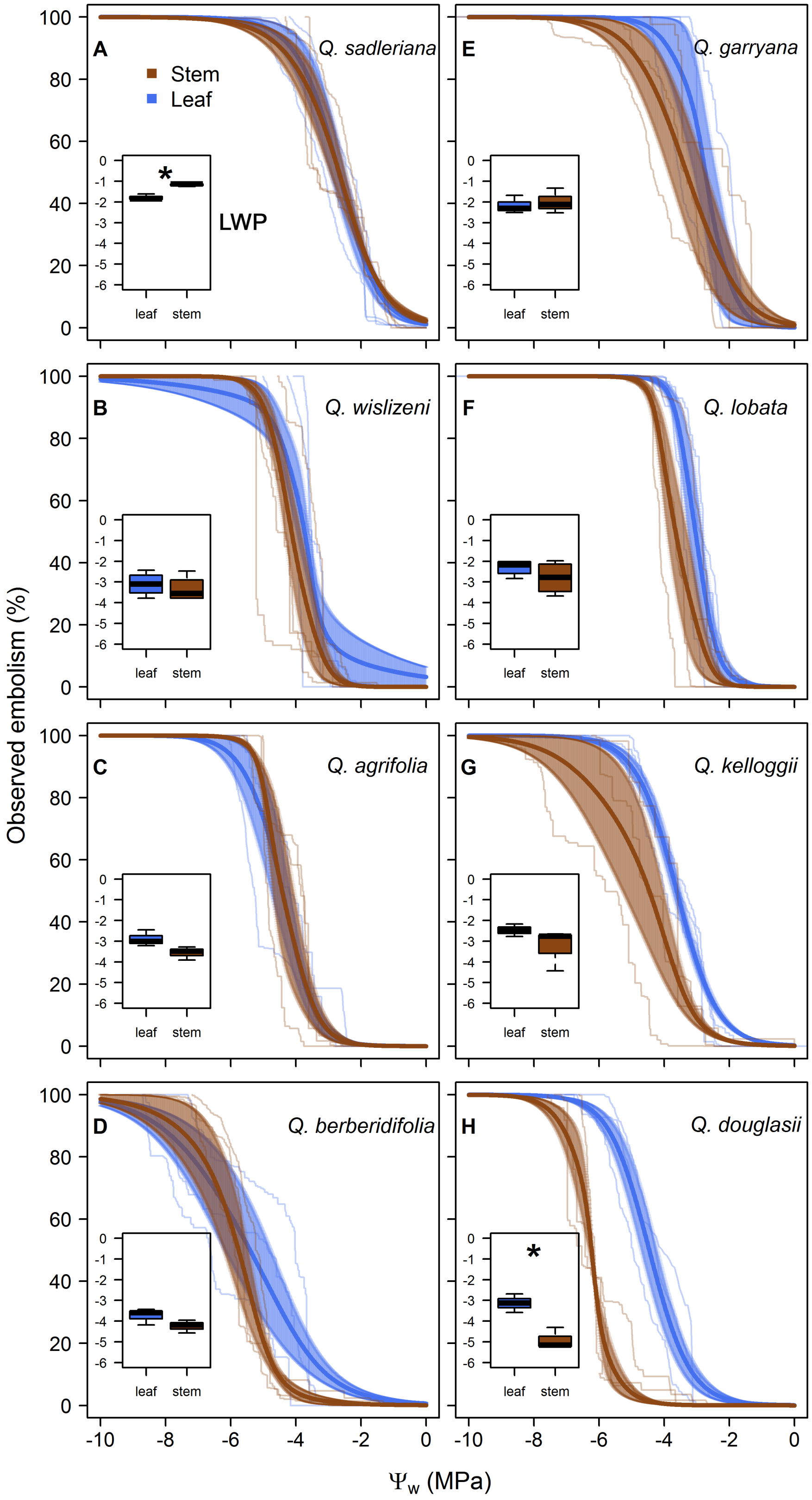

Figure 2: Optical vulnerability curves for leaves (blue) and stems (brown) for all eight sample *Quercus* species: *Q. sadleriana* (A, the least resistant to embolism); *Q. wislizenii* (B); *Q. agrifolia* (C); *Q. berberidifolia* (D); *Q. garryana* (E); *Q. lobata* (F); *Q.kelloggii* (G); and *Q. douglasii* (H). Solid dark lines and the shading indicates the mean observed embolism and s.e. for each tissue type (n = 3). Light lines indicate raw curves for each individual. The insets in each panel are boxplots showing the mean air entry water potential (P_e) for each tissue of each species. Asterisks indicate significant differences between tissues.

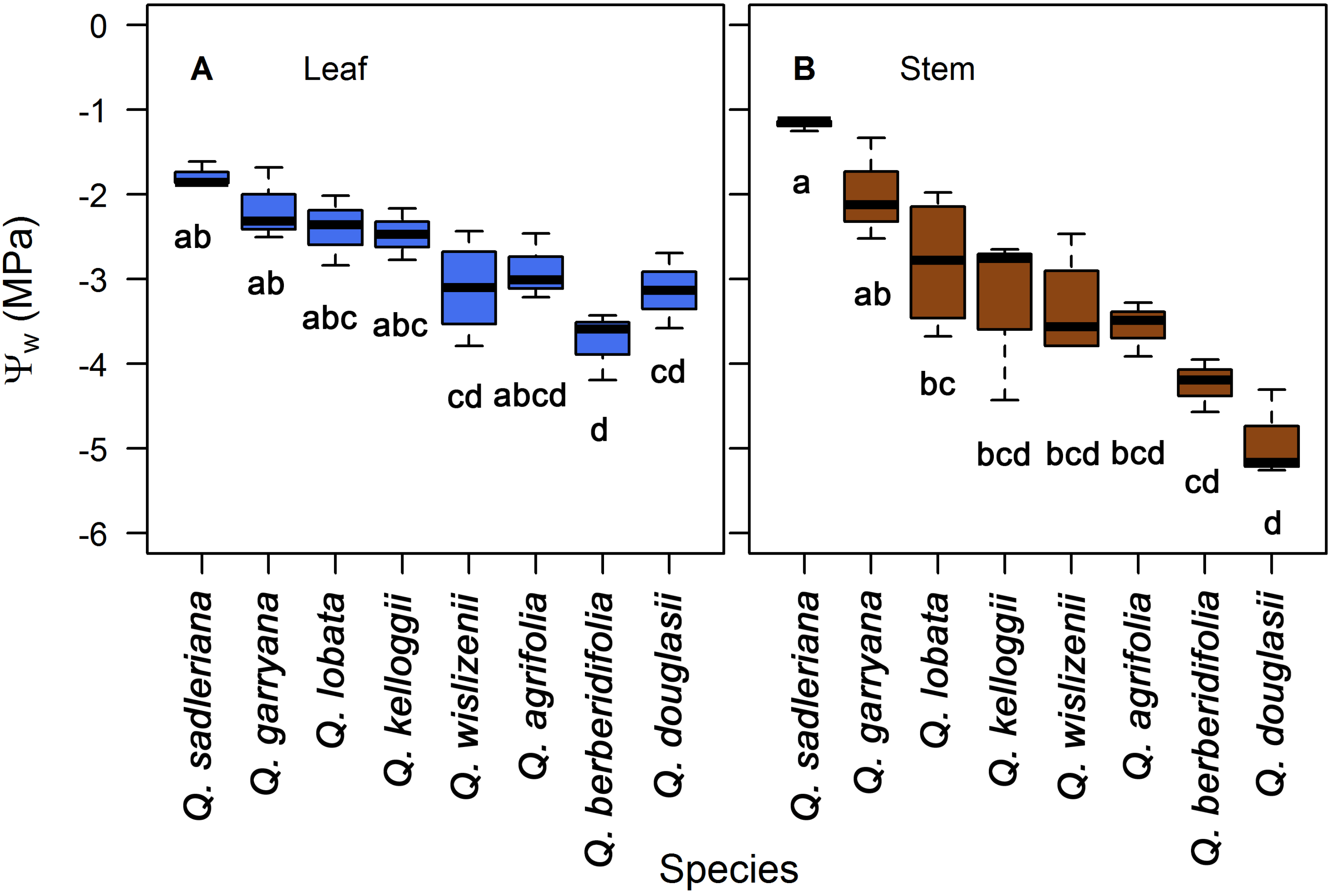

Figure 3: Inter-specific comparisons of the air-entry water potential (P_e; mean ± s.e; n = 3) for leaves (A) and stems (B). Letters below each boxplot indicate significant differences between species.

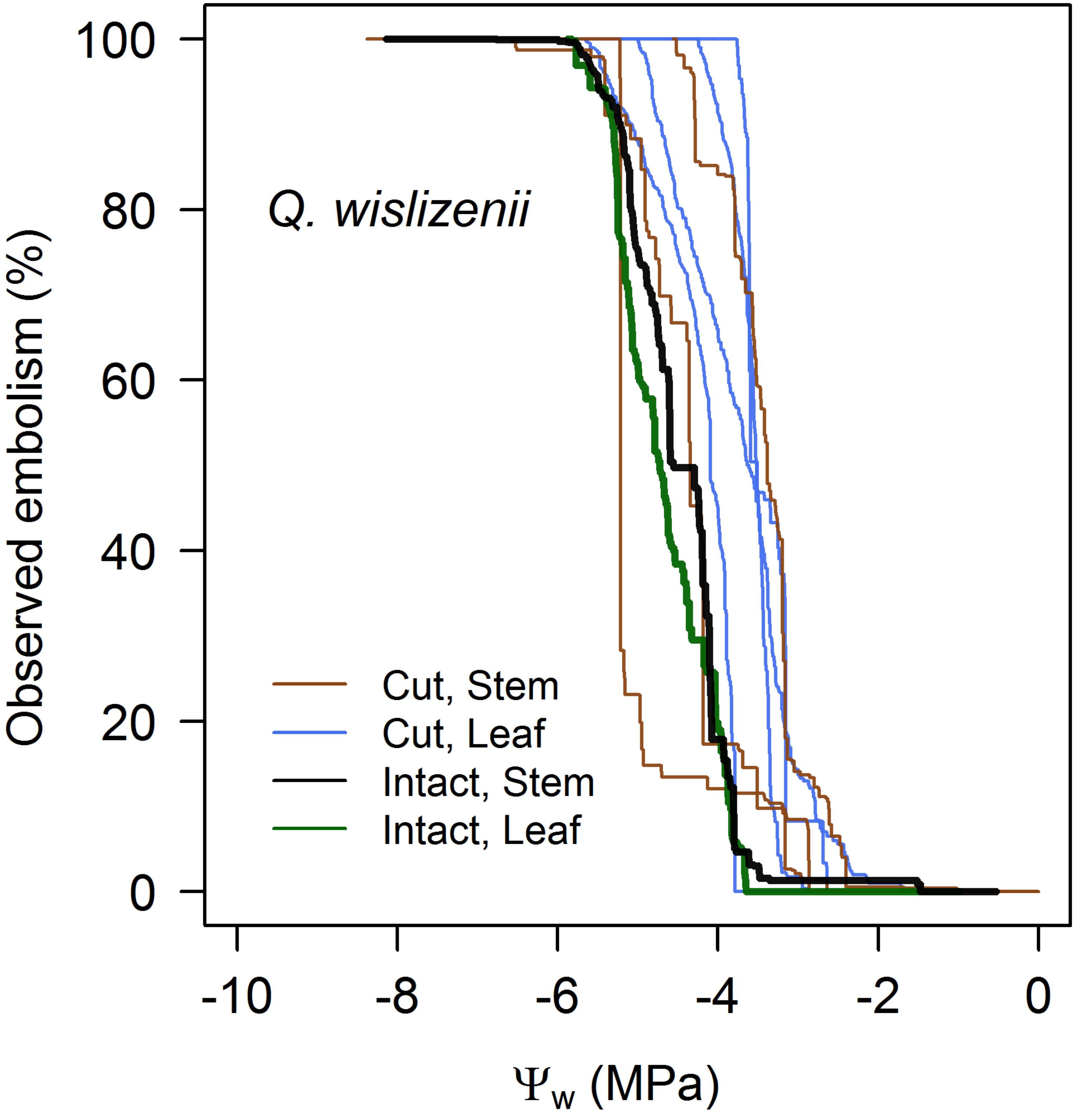

Figure 4*:* A comparison of vulnerability curves generated on cut leaves and branches and a leaf and branch of a fully intact, well-watered *Quercus wislizenii* individual that had experienced no prior water stress.

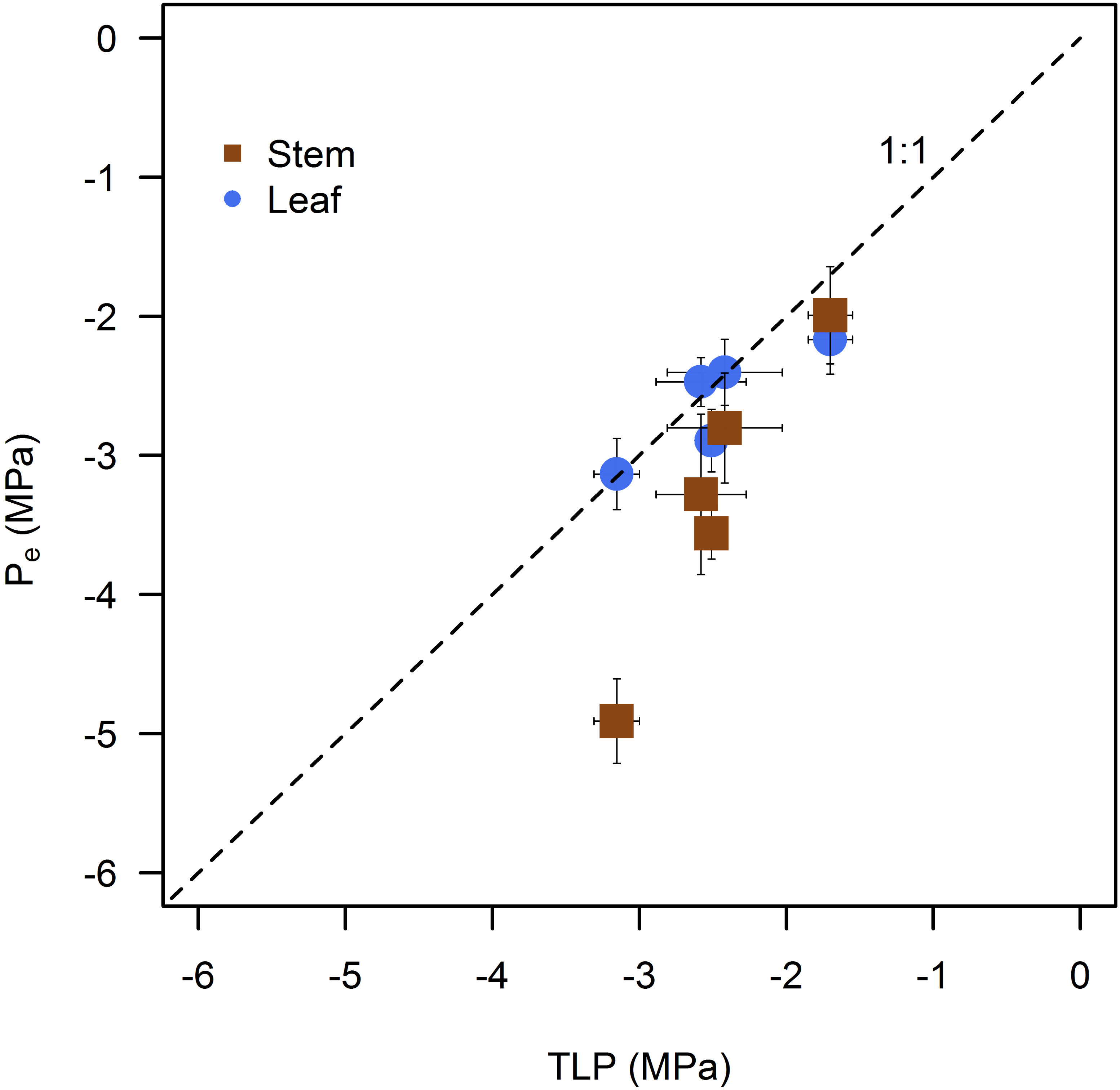

Figure 5: A comparison of turgor loss point (TLP; mean ± s.e; n = 3) and air-entry water potential (P_e) of leaves (blue; mean ± s.e; n = 3) and stems (brown; mean ± s.e; n = 3) of five sample *Quercus* species, indicating that TLP was reached at higher water potentials than P_e of leaves and stems of most sample species.

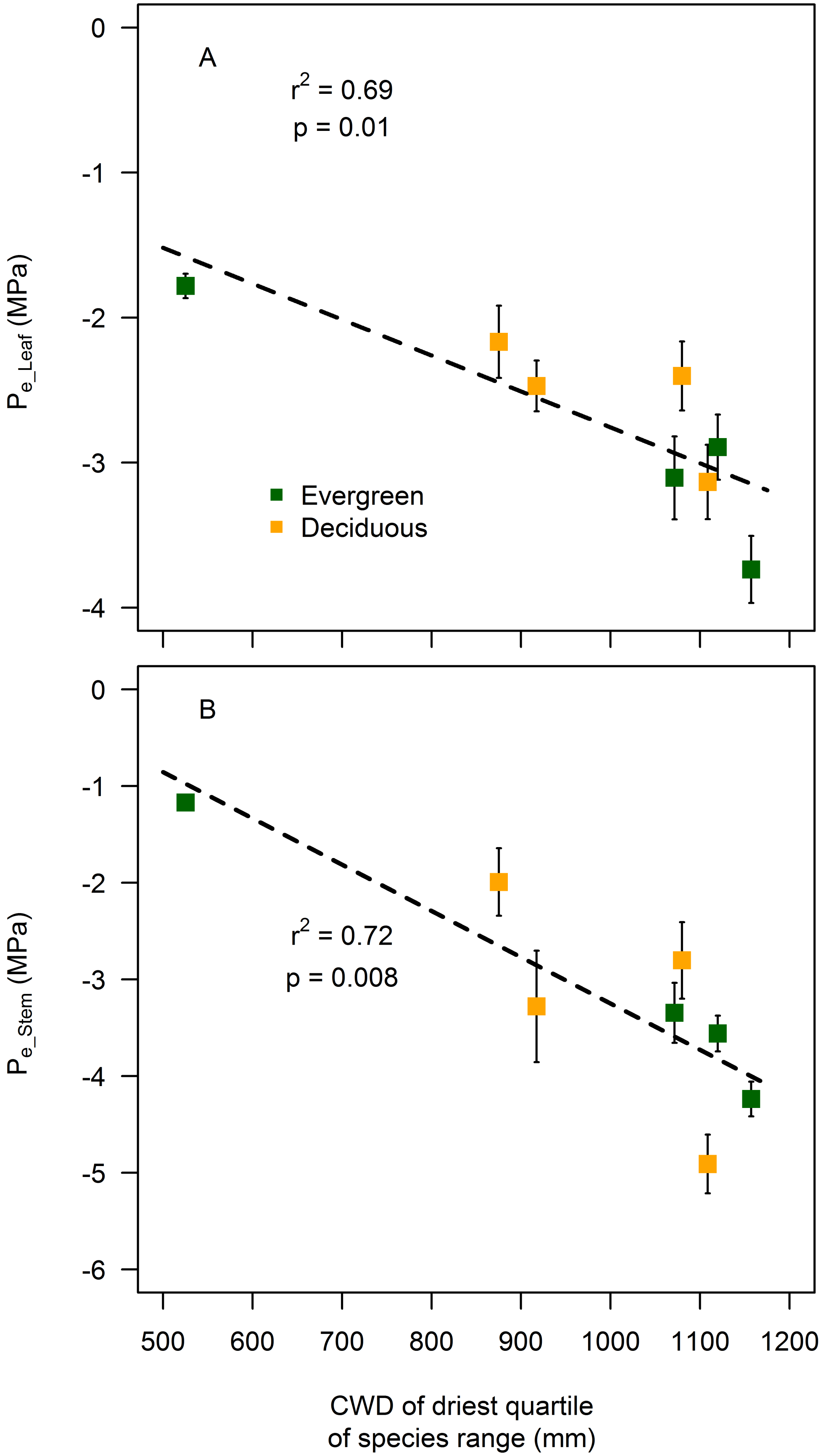

Figure 6: Climatic water deficit (a proxy for the aridity of a site, mm) of the driest 25th percentile of the distribution of our eight sample *Quercus* species is significantly associated with the air entry water potential (P_e; mean ± s.e; n = 3) of both leaves (A) and stems (B). Species less resistant to embolism occur in much more mesic sites in comparison to species that have greater resistance to embolism.

Parsed Citations

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