

HYDRAULICS OF *PINUS* (SUBSECTION PONDEROSAE) POPULATIONS ACROSS AN ELEVATION GRADIENT IN THE SANTA CATALINA MOUNTAINS OF SOUTHERN ARIZONA

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ABSTRACT

The ability of plants to tolerate and recover from periodic water stress affects their competitive ability, survival, and distribution, leading to shifts in plant communities as environmental conditions change. We investigated the hydraulic traits of two closely related *Pinus* taxa to assess population and taxonomic variability in plant hydraulic traits. We hypothesized that traits would vary with elevation but exhibit similar traits where taxa co-occurred. We measured predawn and midday leaf pressure potential (Ψ_p) across three seasons, xylem specific hydraulic conductivity (K_s), and vulnerability to xylem embolism (P_{50}). These were measured on *Pinus ponderosa* var. *brachyptera* (Engelm.) Lemmon that occurred at a high elevation site (2770 m), *P. arizonica* Engelm. at a low elevation site (2135 m), and both species where they co-occurred at the mid-elevation site (2475 m) in the Santa Catalina Mountains of southern Arizona. Plants from the high elevation site had the least negative Ψ_p and the highest K_s . The two taxa differed from one another when compared between the high and low elevation sites, but they were not different where they co-occurred. The two *Pinus* taxa show plasticity in their hydraulic traits across sites. Conditions across the elevational gradient appear to lead to a convergent solution in hydraulic traits for these taxa where their ranges overlap but differences in traits where they do not overlap. Increasing aridity in the region could lead to shifts in suitable habitat, reduced water transport ability at range margins, and shifts in population distributions.

Key Words: cavitation resistance, elevation, embolism, hydraulic traits, Ponderosae, xylem conductivity, water potential.

Long-lived woody plants persist for long periods of time and through varying conditions. The abilities of plants to efficiently transport water and to withstand hydraulic transport failure in response to periodic water stress are important determinants of their ability to tolerate the long-term extreme conditions of a particular site and to successfully compete for limited resources. Resistance to water stress-induced xylem embolism is an important plant functional trait that varies across broad scales and is linked to functional differences among ecosystems (Maherali et al. 2004; Choat et al. 2012) and plant communities (Jacobsen et al. 2007; Hacke et al. 2009). Across the ranges of individual species, variation in embolism resistance has been found between populations in some species (Mencuccini and Comstock 1997; Kavanagh et al. 1999; Kolb and Sperry 1999; Pratt et al. 2012; Jacobsen et al. 2014). Efficiency of hydraulic transport is also an important trait that varies across landscapes and ecosystems (Gleason et al. 2016) and may vary between populations growing in different environmental conditions (Maherali and DeLucia 2000).

However, relatively little is known about hydraulic functional plasticity and population variation, and this area of study was recognized as particularly

limited in two recent reviews (Jacobsen et al. 2014; Anderegg 2015). These have also been identified as key areas of inquiry where more information is required to better understand plant response to drought (Choat et al. 2012; Anderegg 2015). Species plasticity and population variability may also dramatically impact predictions of species responses to climate change (Valladares et al. 2014), which could alter adaptation and mitigation strategies.

Within *Pinus*, evidence of population divergence in hydraulic traits has been mixed. Some studies have found that populations of Scots pine (*P. sylvestris* Baumg.) (Martínez-Vilalta and Piñol 2002; Martínez-Vilalta et al. 2009) and maritime pine (*P. pinaster* Loudon) (Lamy et al. 2014) have little variation in hydraulic conductivity or cavitation resistance. In contrast, studies on other *Pinus* species have found that some hydraulic traits do appear to vary among populations, including in Aleppo pine (*P. halepensis* M.Bieb.) (Tognetti et al. 1997; David-Schwartz et al. 2016), ponderosa pine (*P. ponderosa* Douglas ex. P. Lawson & C. Lawson) (Maherali and DeLucia 2000), and Canary Island pine (*P. canariensis* C.Sm. ex DC.) (López et al. 2016). Furthermore, several studies have confirmed a link between drought and pine species distributions, suggesting that hydraulic

traits may be important determinants of species and populations distributions and structure (Allen and Breshears 1998; Bigler et al. 2006; McDowell et al. 2009).

Within the Santa Catalina Mountains of southern Arizona, two closely related *Pinus* taxa within the subsection Ponderosae turn over along a topographical, microhabitat, and elevational gradient (Kearney and Peebles 1961; Peloquin 1984; Epperson et al. 2001; Marquardt et al. 2019). At higher elevations (2500–2650 m), which are cooler and more mesic, trees from the taxon previously described as Rocky Mountain ponderosa pine (*P. ponderosa* Lawson & C. Lawson var. *scopulorum* Engelm.) are the sole pines (Kearney and Peebles 1961; Kilgore, 2007). Although this taxon has predominantly three needles per fascicle (Conkle and Critchfield 1988), a recent study confirms that this taxon is not var. *scopulorum* Engelm., but rather more closely related to the Ponderosae of northern Mexico (Epperson et al. 2009; Willyard et al. 2017; Marquardt et al. 2019) and based on DNA and morphological characteristics was recognized as *P. ponderosa* var. *brachyptera* (Engelm.) Lemmon by Willyard et al. (2017). Herein, this taxon is referred as *P. ponderosa*. At lower elevations (1760–2400 m), which are warmer and more xeric, Arizona pine (*P. arizonica* Engelm.) is dominant; this taxon is closely related to *P. ponderosa* and has been classified by some as a subspecies (*P. ponderosa* var. *arizonica* (Engelm.) Shaw) (Kral 1993), although current classifications recognize it as a separate species (Price et al. 1998; Willyard et al. 2017) that is part of the ponderosa pine complex. *Pinus arizonica* has predominantly five needles per fascicle. At mid-elevations of this gradient (2430–2550 m), these taxa co-occur (Epperson et al. 2001; Kilgore 2007).

We examined the hydraulic traits of these two closely related taxa at both higher and lower elevation sites where they are mono-specific and within the mid-elevation transition zone where the two taxa co-occur. We predicted that hydraulic traits would differ between the mono-specific populations of the two taxa from the extremes of the elevational gradient, but that the co-occurring populations from the two *Pinus* taxa would not differ within the mid-elevation transition zone. This was predicted based on prior studies finding that some *Pinus* species vary in their hydraulic traits between populations and with differing growing conditions, leading to potential differences within a taxa between sites. For taxa at the site where they co-occur, some prior studies have found that *Pinus* species may be quite similar in some of their hydraulics traits when they are growing under the same environmental conditions (Oliveras et al. 2003; Gonzalez-Benecke et al. 2011). Trees growing at higher elevation were predicted to display hydraulic traits consistent with the more mesic environment than trees growing in more arid conditions at lower elevation. We measured embolism resistance (P_{50}), xylem specific hydraulic con-

ductivity (K_s), and seasonal leaf pressure potentials (Ψ_p).

METHODS

Study site and tree selection

The Santa Catalina Mountains rise from a basal elevation of 760 m to 2791 m at the highest point on Mount Lemmon in southern Arizona. Approximately 60% of the precipitation occurs during the summer monsoon season (July–September) with the remaining precipitation arriving during the winter months (Sheppard et al. 2002). The driest part of the year is the foresummer (May–June).

We investigated two closely related *Pinus* taxa within subsection Ponderosae at three sites across a moisture and elevational gradient. The high-elevation site contains only *P. ponderosa* and is near the summit of Mount Lemmon (32.4396°N 110.7871°W, 2770 m) with an interpolated (Wang et al. 2016) mean annual temperature (MAT) of 17.6°C and mean annual precipitation (MAP) of 569 mm for the period 1971–2000. The mid-elevation site contains both species and is located upslope from the Palisade Ranger Station (32.4138°N 110.7149°W, 2475 m), with a MAT of 18.4°C and MAP of 610 mm. The low-elevation sites contain only *P. arizonica* and are located near Lizard Rock (32.3844°N 110.6930°W, 2135 m) and Rose Canyon (32.3967°N 110.6932°W, 2165 m), with an average MAT of 19.1°C and MAP of 516 mm. In the years just prior to our measures (2001–2005), the high elevation site received 678 mm of annual precipitation (Mt. Lemmon ALERT Gauge, Pima County, AZ), and the mid-elevation site received 669 mm (White Tail ALERT Gauge, Pima County, AZ). For these years, we do not have climate data for the low elevation site, but it was markedly more arid than the other sites.

At each site, we identified trees by taxon and selected trees of similar size (mean tree height of 3.7 m and DBH of 12.6 cm) for measurements. Taxonomy was determined by their mean number of needles per fascicle across 5 yr of needles on at least one terminal branch because needle number separates these taxa, with *P. ponderosa* containing less than 3.2 needles per fascicle, while *P. arizonica* contains greater than 4.6 needles per fascicle (Peloquin 1984). We focused our sampling on trees with 3 needles per fascicle (*P. ponderosa* var. *brachyptera*) or five needles per fascicle (*P. arizonica*) to ensure that we were sampling individuals of known identity. Trees with intermediate or mixed needle number were not selected because they may represent hybrids (Peloquin 1984; Rehfeldt et al. 1996; Epperson et al. 2001, 2009).

Leaf Pressure Potentials

Leaf pressure potentials (Ψ_p) were measured from each of 3–8 trees per site and taxon in a single day

during the arid foresummer (10–20 June 2005), late summer monsoon wet season (6–12 August 2005), and winter (24–27 January 2006). From each tree, 5–10 current-year fascicles were collected from the terminal shoot on the second-lowest living branch (1.0–1.5 m above ground) on the south side of the tree at predawn and midday. Fascicles were cut from the tree using a fresh razor blade, placed in a plastic bag, and stored in a cooler with ice packs. Within 2.5 hrs of collection, Ψ_p from the fascicles were measured using a pressure chamber (PMS Instruments, Inc., Corvallis, OR). We measured several fascicles per tree to ensure that we were obtaining consistent values and then averaged samples by tree.

Stem Hydraulics

Stems were collected in the field on 20 and 26 October 2005 for determination of xylem specific hydraulic conductivity and vulnerability to cavitation. At predawn to early morning on each collection day, 5–11 trees per taxon per site were selected. From each tree, stems from the lowest living branch that were 5–10-mm diameter with minimal curvature were cut to 0.5 m in length, double-bagged in plastic bags with a moist paper towel, placed on ice, and transported via overnight shipping to Michigan State University. Stems were measured immediately following their arrival and within 3 d of collection.

In the laboratory, stems were trimmed under water from each end until a straight, unbranched segment 6–9 mm in diameter and 14 cm in length was obtained. Stems were then connected to a tubing system and flushed with low pH degassed water (pH 2 HCl; Sperry and Saliendra 1994; Sperry and Ikeda 1997; Pockman and Sperry 2000; Sperry et al. 1994) that had been passed through a 0.1- μ m filter. Stems were flushed for 1 hr at 30 kPa to remove gas emboli from stems (Hacke et al. 2000a; Hacke et al. 2007). This relatively low pressure was used in order to avoid aspiration of tori in pit membranes (Sperry et al. 2005). Conductivity increased with flushing. Following the initial one hour flush, hydraulic conductivity (K_h) of stems was measured, and stems were flushed for additional 20-min intervals until a constant maximum hydraulic conductivity (K_{hmax}) was obtained (usually less than 2 hr) (Hacke and Jansen 2009; Schoonmaker et al. 2010). Hydraulic conductivity of stems was measured gravimetrically (Sperry et al. 1988) using an analytical balance (Model BP 121 S, Sartorius AG, Goettingen, Germany) and a pressure head of <2 kPa. Conductivity was corrected for background flows (Hacke et al. 2000b). Xylem specific hydraulic conductivity (K_s) of stems was determined using the K_{hmax} and the cross-sectional xylem area. Cross-sectional xylem area (minus the pith) was determined for each stem. The K_{hmax} was then divided by this area for each stem to yield the xylem specific conductivity ($\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$). For K_s , 7–11 individuals were measured per site and taxon.

Following determination of K_s , a subset of stems (5–8 per species and site) were measured using a standard centrifuge technique (Alder et al. 1997) to generate vulnerability to cavitation curves. Stems were spun in a centrifuge (Sorvall RC-5B, DuPont Instruments, Wilmington, DE) using a custom-built rotor in order to generate known negative pressures. Stems were then reconnected to the tubing system, and the new hydraulic conductivity (K_s) was determined. This process was repeated with successive spins generating more negative pressures until stems experienced $>80\%$ loss in hydraulic conductivity. Vulnerability to cavitation curves were constructed by plotting the water potential (generated using the centrifuge) versus hydraulic conductivity, and the pressure at which 50% loss in conductivity occurred for each sample (P_{50}) was obtained for each sample using a Weibull curve (Microsoft Excel 2010, Microsoft, Redmond, WA). When comparing curves across the taxa and sites, curves were plotted as the water potential versus K_s because several studies have now highlighted the importance of consideration of K_s when comparing across curves and the potential difficulty in interpreting and evaluating curves that show only relative losses (Sperry et al. 2012; Jacobsen and Pratt 2012; Hacke et al. 2015).

Data Analyses

The elevational range for each taxon overlapped, with the ends of the ranges occupied by only one taxon. Because of the nature of these distribution limits for each species, with both species not occurring across all three sites, the effects of site (i.e., comparing across the low, mid, and high elevation sites) could not be examined across the entire study nor could an interaction between site and taxon be evaluated. This limitation was part of the original study design and did not impact the comparisons that we were most interested in, which were pre-planned contrasts of hydraulic trait variation between the two taxa from their mono-specific populations and the two taxa at the site where they co-occurred. Consequently, our analyses included each taxon \times site as a separate treatment (i.e., we ran an ANOVA comparing data from four groups: *P. ponderosa* at the upper site, *P. ponderosa* at the mid site, *P. arizonica* at the mid site, and *P. arizonica* at the lower site). This approach allowed us to calculate the correct error term across the analysis, while analyzing the contrasts that were the focus of the present study. This analysis precluded a comparison of the two taxa pooled across the sites at which they occurred, but this comparison was not important for addressing our experimental question. We used an alpha of 0.5 for our ANOVA and conducted comparisons among groups using Tukey Pairwise comparisons. All analyses were run using Minitab 17 (v. 17.2.1, Minitab, Inc., State College, PA, USA).

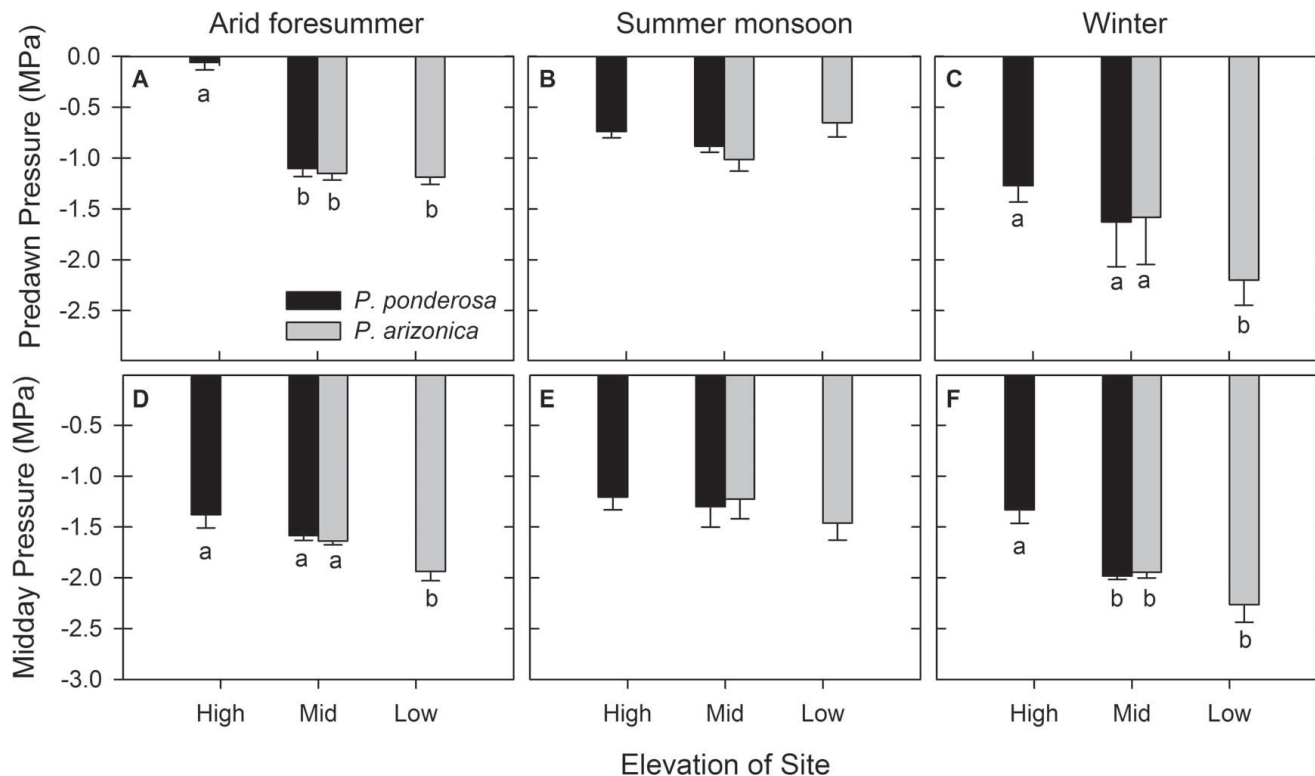


FIG. 1. The seasonal mean (± 1 SE) leaf pressure potentials at predawn (A–C) and midday (D–F) for two *Pinus* taxa, *P. ponderosa* and *P. arizonica*, from sites at three different elevations (High, Mid, and Low) across three seasons (Arid foresummer, Summer monsoon, and Winter). For panels A, C, D, and F, bars with different lowercase letters are significantly different. There were no significant differences among taxa and sites for the data shown in panels B and E.

RESULTS

Leaf Pressure Potentials

Trees from higher elevation had significantly higher Ψ_p than trees from lower elevations at predawn and midday during the arid foresummer (Fig. 1A) and winter (Fig. 1F). The trees at the lowest elevation had significantly more negative Ψ_p at midday during the arid foresummer (Fig. 1D) and predawn during the winter (Fig. 1C). Where they co-occurred at the mid-elevation site, Ψ_p were not different between the taxa during any of the sampled periods (Fig. 1; Table 1).

Pressure potentials were most negative for both taxa in the winter and least negative during the monsoon season, with the arid foresummer intermediate. There were no differences between taxa or sites during the moist monsoon season (Fig. 1B, E; $F_{3,18} = 2.01$, $P = 0.149$, predawn; $F_{3,18} = 0.18$, $P = 0.907$, midday). However, there were differences among sites and taxa during the arid foresummer (Fig. 1A, D; $F_{3,18} = 8.28$, $P = 0.001$, predawn; $F_{3,18} = 8.32$, $P = 0.001$, midday) and winter (Fig. 1C, F; $F_{3,18} = 11.11$, $P < 0.001$, predawn; $F_{3,16} = 15.64$, $P < 0.001$, midday).

TABLE 1. PREDAWN AND MIDDAY LEAF PRESSURE POTENTIALS (MPa; MEAN \pm 1 SE) FOR TWO *PINUS* TAXA, *P. PONDEROSA* AND *P. ARIZONICA*, FROM SITES AT THREE DIFFERENT ELEVATIONS (HIGH, MID, AND LOW) ACROSS THREE SEASONS (ARID FORESUMMER, SUMMER MONSOON, AND WINTER). Each taxon only occurred across two of the sampled elevations, and N/A is reported if a taxon did not occur at a given site. Significant differences between sites and species within a season are shown in Fig. 1.

| Site | Arid foresummer | | Summer monsoon | | Winter | |
|---------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| | <i>P. ponderosa</i> | <i>P. arizonica</i> | <i>P. ponderosa</i> | <i>P. arizonica</i> | <i>P. ponderosa</i> | <i>P. arizonica</i> |
| Predawn | | | | | | |
| High | -0.06 ± 0.08 | N/A | -0.74 ± 0.06 | N/A | -1.38 ± 0.13 | N/A |
| Mid | -1.10 ± 0.08 | -1.15 ± 0.07 | -0.88 ± 0.06 | -1.01 ± 0.11 | -1.59 ± 0.05 | -1.64 ± 0.04 |
| Low | N/A | -1.19 ± 0.07 | N/A | -0.65 ± 0.14 | N/A | -1.94 ± 0.09 |
| Midday | | | | | | |
| High | -1.27 ± 0.16 | N/A | -1.21 ± 0.12 | N/A | -1.33 ± 0.13 | N/A |
| Mid | -1.63 ± 0.44 | -1.58 ± 0.47 | -1.30 ± 0.20 | -1.23 ± 0.19 | -1.98 ± 0.03 | -1.95 ± 0.06 |
| Low | N/A | -2.20 ± 0.25 | N/A | -1.46 ± 0.17 | N/A | -2.26 ± 0.17 |

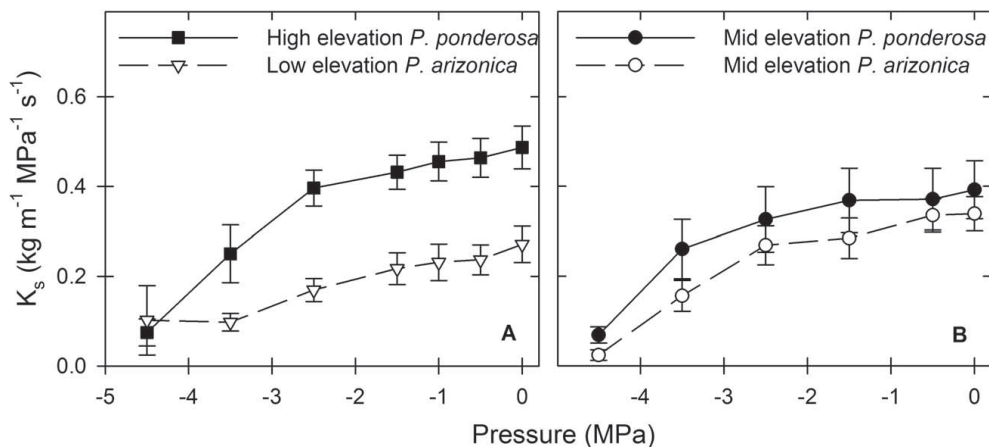


FIG. 2. Vulnerability to cavitation curves for two *Pinus* taxa, *P. ponderosa* and *P. arizonica*, with the decline in mean (± 1 SE) xylem specific conductivity (K_s) with pressure for three different sites: (A) a high elevation site containing only *P. ponderosa* compared to a low elevation site containing only *P. arizonica*, and (B) a mid-elevation site where both taxa co-occur.

Stem Hydraulics

Vulnerability to cavitation curves varied for the two taxa depending on site (Fig. 2; Table 2). When the two taxa were compared from the two sites where each occurred mono-specifically (i.e., *P. ponderosa* at the upper site compared to *P. arizonica* at the lower site), the curves of the two taxa varied greatly (Fig. 2A). In contrast, when the curves for these two taxa were plotted from individuals measured from the mid elevation site where they both co-occurred, there was no difference between the curves of the two species (Fig. 2B).

K_s varied significantly with taxon by site (Fig. 3A; Table 2; $F_{3,30} = 4.75$, $P = 0.008$). Consistent with the pattern evident from the vulnerability to cavitation curves, K_s was significantly different when the two taxa were compared from the high and low elevation sites where they each occurred mono-specifically, but they were not different from one another at the mid elevation site where they co-occurred. P_{50} did not vary with taxon by site (Fig. 3B; $F_{3,23} = 1.03$, $P = 0.399$). This may have been due to the smaller sample size for this comparison because K_s and P_{50} were strongly correlated suggesting that changes in K_s should have corresponded to changes in P_{50} . K_s was predictive of P_{50} for *P. ponderosa* (Fig. 4; $F_{13} = 5.70$, $P = 0.034$, $r^2 = 0.32$) and for all of the data pooled across all sites and taxa ($F_{23} = 10.90$, $P = 0.003$, $r^2 = 0.33$), but not

for the *P. arizonica* analyzed alone ($F_9 = 1.32$, $P = 0.285$, $r^2 = 0.14$). K_s was negatively correlated with P_{50} , such that increased K_s corresponded to a decreased (i.e., more negative) P_{50} .

DISCUSSION

We found that the comparative hydraulic traits of two closely related *Pinus* taxa differed depending on where they were sampled. When they were compared using data gathered from trees occurring at a high elevation and low elevation site where the taxa do not co-occur, the taxa significantly differed in their hydraulic conductivity. When these two taxa were compared at a mid-elevation site where they co-occurred, the taxa were not different in their hydraulic conductivity. This variation in traits within taxa from populations experiencing different climatic conditions and occurring at different sites is consistent with several studies on both gymnosperm (Tognetti et al. 1997; Maherali and DeLucia 2000; Martínez-Vilalta et al. 2009) and angiosperm (Mencuccini and Comstock 1997; Kavanagh et al. 1999; Kolb and Sperry 1999; Pratt et al. 2012; Jacobsen et al. 2014) species. However, this variability may be species or population specific, and several studies have found that hydraulic traits did not vary among studied populations (Mencuccini and Comstock

TABLE 2. MEAN (± 1 SE) XYLEM SPECIFIC CONDUCTIVITY (K_s) AND PRESSURE AT 50% LOSS IN HYDRAULIC CONDUCTIVITY (P_{50}) FOR TWO *PINUS* TAXA, *P. PONDEROSA* AND *P. ARIZONICA*, FROM SITES AT THREE DIFFERENT ELEVATIONS (HIGH, MID, AND LOW). Each taxon only occurred across two of the sampled elevations, and N/A is reported if a taxon did not occur at a given site. Significant differences between sites and species within a season are shown in Fig. 3.

| Site | K_s ($\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$) | | P_{50} (MPa) | |
|------|--|---------------------|---------------------|---------------------|
| | <i>P. ponderosa</i> | <i>P. arizonica</i> | <i>P. ponderosa</i> | <i>P. arizonica</i> |
| High | 0.48 ± 0.03 | N/A | -3.43 ± 0.23 | N/A |
| Mid | 0.36 ± 0.07 | 0.34 ± 0.04 | -3.36 ± 0.18 | -3.15 ± 0.21 |
| Low | N/A | 0.26 ± 0.04 | N/A | -2.95 ± 0.13 |

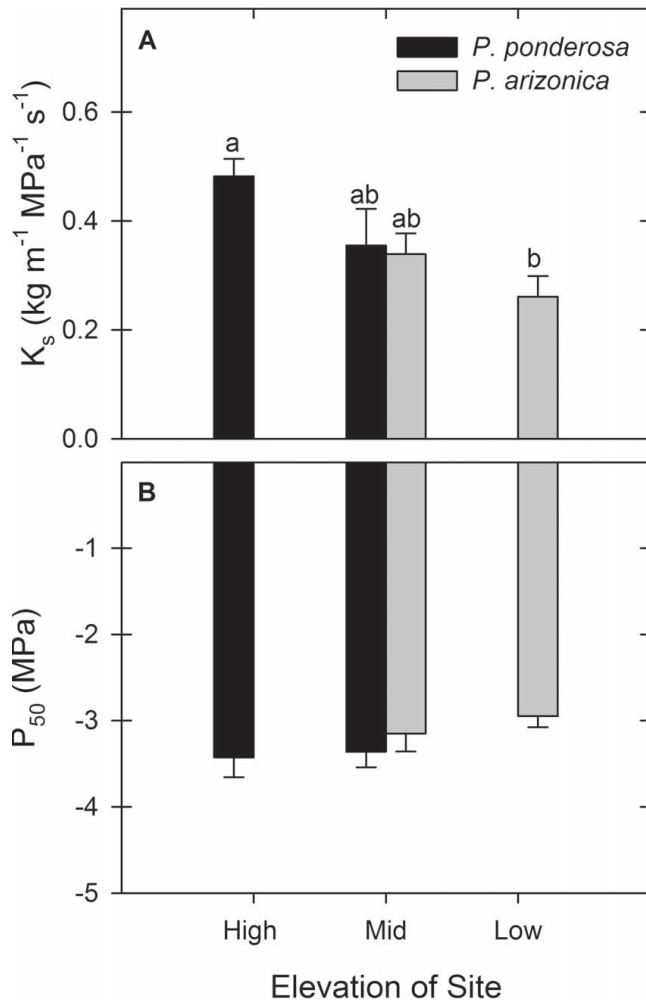


FIG. 3. The mean (± 1 SE) (A) xylem specific conductivity (K_s) and (B) pressure at 50% loss in hydraulic conductivity (P_{50}) for two *Pinus* taxa, *P. ponderosa* and *P. arizonica*, from across an elevation gradient. For panel A, bars with different lowercase letters are significantly different. There were no significant differences among taxa and sites for the data shown in panel B.

1997; Matzner et al. 2001; Martínez-Vilalta and Piñol 2002; Stout and Sala 2003; Lamy et al. 2011).

The different hydraulic traits occurring across the studied elevation transect may be due to either plasticity in xylem structure and functional or genetic variation among populations. In *P. ponderosa*, a previous study found differences in hydraulic conductivity among desert and montane populations, but these differences were not maintained in a common garden, suggesting that they were due to xylem plasticity (Maherali and DeLucia 2000). For another species, *P. halepensis*, hydraulic trait differences were found in common garden experiments, suggesting that there was genetic variation in hydraulic traits among populations (Tognetti et al. 1997; David-Schwartz et al. 2016). Common garden and controlled experiments will likely be instrumental in future studies examining the ability of plants to respond to varying conditions and the impact of plasticity versus genetics in confirming field-based findings of variation (Holste et al. 2006; Beikircher

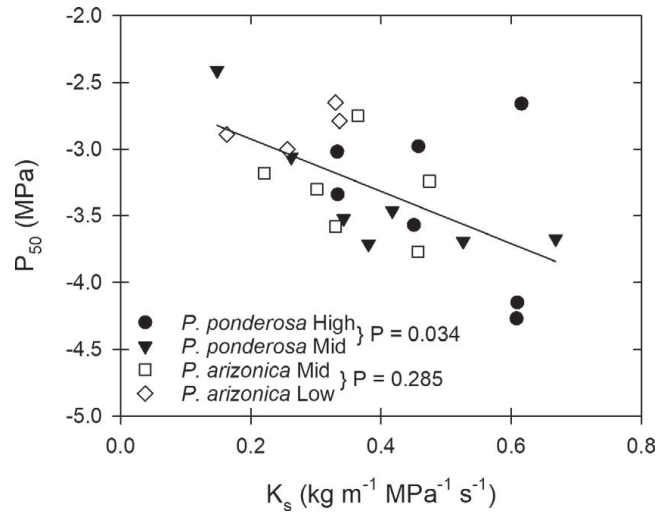


FIG. 4. Xylem specific conductivity (K_s) as a predictor for the pressure at 50% loss in hydraulic conductivity (P_{50}) for two *Pinus* taxa, *P. ponderosa* (filled circles) and *P. arizonica* (open circles). K_s was predictive of the pressure at 50PLC for *P. ponderosa* (solid line) but not for *P. arizonica*.

and Mayr 2009; Mayr et al. 2010; Fichot et al. 2010; Awad et al. 2010; Plavcová and Hacke 2012).

In the present study, both taxa exhibited similar hydraulic traits at the site where they co-occurred. This suggests that there may be a common “solution” for *Pinus* for persistence within the conditions of that specific site. Both taxa were able to occur there because they were each able to achieve this specific functional trait value. The transition zone may, therefore, be delimited by limits on the ability of each taxon to further respond to changing climate conditions, which prevented the *P. ponderosa* from moving into sites any farther downslope or the *P. arizonica* from moving upslope. Their co-occurrence also suggests that competition between the two may be limited and that physiological tolerance traits are key in determining distributions in this system.

Hydraulic tolerances of *Pinus* species may be particularly important due to their apparent sensitivity to drought and water stress. The K_s and P_{50} for the taxa included in this study are similar to those previously reported for *Pinus ponderosa* (Maherali and DeLucia 2000; Stout and Sala 2003). Several studies have described recent mortality events of *Pinus* that have been associated with water stress (Allen and Breshears 1998; Bigler et al. 2006; McDowell et al. 2009). In the present study, water potentials were relatively high compared to the cavitation resistance of plants, although our study did not occur during a particularly dry year. However, plants may have very different tolerances of embolism. For instance, some desert plants appear to regularly reach very high levels of embolism without experiencing dieback or mortality (Jacobsen et al. 2007; de Dios Miranda et al. 2010), while other species may be sensitive to lower levels of embolism (~60%) (Sperry and Love 2015).

Absolute levels of conductivity (Sperry et al. 2012; Jacobsen and Pratt 2012; Hacke et al. 2015) are also important to consider, and pines, which have relatively low maximum hydraulic conductivity, may be sensitive to even small declines in supply. The ability to tolerate very low flows, even for brief periods of time, varies among species (Pratt et al. 2005) and links leaf-level traits associated with minimizing water loss to hydraulic supply traits. Compared to *P. ponderosa*, *P. arizonica* is better able to maintain photosynthetic function and limit water loss from needles when dehydrated (Kilgore 2007), which may explain the ability of this species to persist in drier sites or to tolerate the higher levels of embolism and lower hydraulic conductance than it experiences as a result of being both more vulnerable and having lower conductivity.

Another way of examining the hydraulic limits of species is through the hydraulic safety margin, which is the difference between the minimum water potential experienced and vulnerability to embolism (Oliveras et al. 2003; Meinzer et al. 2009; Ramirez et al. 2020). In a recent study comparing the hydraulics of populations, the hydraulic safety margin was useful in identifying intra-specific populations that were hydraulically buffered compared to those that were not (Ramirez et al. 2020). In the present study, high elevation *P. ponderosa* showed the highest hydraulic safety margin and low elevation *P. arizonica* showed the lowest safety margin. For both taxa, the lowest hydraulic safety margins, and most at-risk populations, were those occurring at the lower elevation site for each. This suggests that lower elevation distributions of these species may be most at risk of drought-associated mortality.

In summary, we found evidence of hydraulic trait differentiation between two closely related taxa and hydraulic trait differentiation among populations growing at different elevations. This is an important finding in our developing knowledge of intra-specific variability in plant hydraulic function. The presence of population variability in this and other studies suggests that plant hydraulic studies should more carefully consider these sub-specific patterns in experimental designs and analyses. This may be particularly important in the context of conservation planning and climate change studies because variable versus homogenous species tolerances can greatly alter model outputs (Valladares et al. 2014). This may also be important to consider when examining drought-associated patterns of mortality as linked to functional traits because drought events often affect ecotones and populations at species range margins most strongly (Allen and Breshears 1998; Paddock et al. 2013), and species traits from other populations may not well represent the traits of these susceptible populations.

ACKNOWLEDGMENTS

The authors thank Coronado National Forest (USDA Forest Service) for sampling permits, Steward Observatory

(Univ. of Arizona) for housing, L. Griffith for transportation in Arizona, A. Wigg (Pima County, Arizona) and P. Marquardt (USDA Forest Service) for precipitation data, and S. Blumer, G. Friedlander, and R. Peterson for help with data collection. J. Kilgore and F. Telewski acknowledge support from the Department of Plant Biology and W.J. Beal Botanical Garden at Michigan State University. A. Jacobsen acknowledges support from an NSF-GRF during data collection and from NSF IOS-1252232 and NSF-HRD 1547784 during the analysis and manuscript preparation.

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