



Variation in hydraulic vulnerability of juvenile ponderosa pines in the southwestern United States

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Abstract Hydraulic vulnerability, the sensitivity of xylem embolism to water stress, is a major determinant trait associated with conifer mortality. This study investigated branch P50 (50% hydraulic conductivity loss) of adult and juvenile ponderosa pines across multiple locations in the southwestern United States (SWUS), and examined relationships between P50 and climatic conditions, soil properties and forest management. Juvenile ponderosa pines had significantly more negative P50 values than adults on average. Both age groups exhibited a latitudinal pattern in P50 associated with regional climate conditions. Across the SWUS, juvenile P50

was positively correlated with growing season precipitation and temperature, and negatively correlated with soil pH and clay content. In some cases, significant differences in juvenile P50 between SWUS locations were associated with growing season moisture deficit, whereas other significant differences were less attributable to climate and may attest to potential genetic variation between populations. Climate variation, soil properties and population-level acclimation and/or adaptation may all influence the hydraulic vulnerability of juvenile ponderosa pines in the SWUS, promoting differences in stress tolerance of ponderosa pine forests across the region.

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Introduction

Ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson), a foundational conifer species in mid-elevation forests of the southwestern United States (SWUS), plays a key role in the provision of ecosystem services throughout the region (Pearson 1950; Kolb et al. 2019). The structure, functioning, and composition of ponderosa pine forests has undergone a notable transformation since the mid- to late-nineteenth century, primarily attributed to anthropogenic land and fire management practices. The Euro-American settlement era witnessed a surge in logging, livestock grazing, road construction and mining which, coupled with the suppression of wildfires, promoted a shift towards denser and more uniform forest stands across a significant portion of the ponderosa pine range (Covington and Moore 1994; Rapport 1997). More recently, the resilience of ponderosa pine forests has also been challenged by the escalating frequency and severity

of disturbances including drought, wildfire, and insect outbreaks (Berner et al. 2017; 2019). Recovery of ponderosa pine forests following these disturbances is highly variable (Korb et al. 2019), and model projections suggest that climate change will further restrict recovery by the end of the twenty-first century (Davis et al. 2019). These factors have dramatically increased the vulnerability of ponderosa pine forests over the last century, and the long-term persistence of this foundational species will depend on its ability to withstand multiple and intensifying stress agents.

Regeneration success is critical for ponderosa pine persistence amidst escalating disturbances (Stevens-Rumann et al. 2022), but it is difficult to determine why regeneration is successful in some settings and unsuccessful in others (Puhlick et al. 2012). While studies like Petrie et al. (2023) have shed light on broad-scale environmental conditions associated with recent natural regeneration failure, a deeper understanding of the finer-scale processes and shorter-duration events that influence mortality is lacking, especially at early stages of tree development. Hydraulic failure imposed by water stress and xylem embolism is a key mechanism of conifer mortality during drought (Tyree and Sperry 1989; Adams et al. 2017; Arend et al. 2021). P50, the water potential (MPa) that induces a 50% loss of xylem conductance, is a measure that represents a threshold of tree mortality. More negative P50 values indicate greater levels of embolism resistance (Hacke et al. 2001). A small number of studies have reported differing vulnerability to xylem embolism between adult and juvenile ponderosa pine. Ponderosa pine, like other species, displays a decreasing trend in xylem conduit diameter from roots to trunks to branches, which coincides with the observed decrease in vulnerability to embolism from roots to branches (Domec et al. 2009; Olson et al. 2021). Domec and Gartner (2003) found that adult trees are more susceptible to trunk embolism compared to juvenile ones, whereas Domec et al. (2004) found that roots in juvenile trees are more prone to embolism than those in adults. In contrast, embolism vulnerability in branches has been found to have no significant difference between age groups (Domec et al. 2009). The limited number of studies addressing hydraulic vulnerability in ponderosa pine highlights the need for further research to generalize these findings. Furthermore, young ponderosa pines demonstrate higher leaf-specific conductance compared to adult trees (Domec et al. 2005), which suggests a potential reduction in the ability of taller trees to transport water efficiently to their leaves. Evidence suggests that during drought stress, taller trees with low hydraulic conductance and relatively high leaf area compared to shorter trees experience greater limitations on hydraulic function and carbon uptake, leading to increased mortality (Bennett et al. 2015; McDowell and Allen 2015). Understanding the extent to which hydraulic vulnerability of branches differs between adult and juvenile ponderosa pines,

and of juvenile ponderosa pines of different sizes, therefore, illuminate important components of tree survival, regeneration success and forest persistence.

Meteorological conditions, soil properties and stand characteristics can influence resistance to xylem embolism through their effects on water demand and soil moisture deficit. For example, trees growing in locations with higher aridity develop more resistance to xylem embolisms, i.e., more negative P50 values (Stojnić et al. 2018; Oyanoghafo et al. 2021; Weithmann et al. 2022). Greater resistance to xylem embolism has been associated with vegetation growing on finer textured soils with shallower root systems compared to coarser soils (Hacke et al. 2000; Sperry and Hacke 2002). Recent research also suggests that soil pH might influence drought response. Secchi et al. (2023) found that plants growing in alkaline soils accumulate more osmolytes (i.e., desiccation protective molecules) in their tissues and xylem sap and have faster stomatal closure under water stress. Moreover, studies on drought-induced tree mortality (Bottero et al. 2017; Venturas et al. 2021) reveal that lower-density forests experience less stress during drought due to increased water availability and reduced competition between adult trees, highlighting the importance of forest thinning management strategies to mitigate drought stress (Sohn et al. 2016). In total, a variety of studies have linked meteorology, soil properties and forest management treatments to hydraulic vulnerability, but their effects have not been evaluated in a single study, or across multiple populations growing under different combinations of these factors.

Although ponderosa pine exhibits morphological trait variations (Kolb et al. 2016; Putz et al. 2021), its hydraulic properties, such as vulnerability to xylem embolism, do not necessarily follow a predictable response to landscape attributes (Maherali and DeLucia 2000; Maherali et al. 2002; Clute et al. 2021). Furthermore, although a number of studies have investigated the hydraulic vulnerability of mature ponderosa pine and other conifer species (Maherali and DeLucia 2000; Anderegg and Hillerislambers 2016; Clute et al. 2021), potential differences at early developmental stages are largely unknown, yet may elucidate possible population-level variations in hydraulic stress tolerance that can inform differences in regeneration success observed in the SWUS. In this study, we quantified the hydraulic stress tolerance of adult and juvenile ponderosa pines from three locations in the SWUS and conducted a more detailed analysis of the hydraulic stress tolerance of juvenile ponderosa pines from six locations that exhibited variation in regional climate, soil properties, and management treatments. Our analyses of juvenile ponderosa pines related hydraulic vulnerability to the temperature and water balance characteristics of our six study locations using site characterization data, gridded meteorological estimates, and water balance modeling. We hypothesized that: (1) juvenile

and adult ponderosa pines would exhibit no significant differences in branch vulnerability to xylem embolism (Domec et al. 2009); (2) juvenile ponderosa pines growing in locations with greater meteorological water deficit, greater soil water deficit and higher temperatures would have greater resistance to xylem embolism; (3) juvenile ponderosa pine stands undergoing forest management treatments of thinning for density reduction would have more vulnerable xylem than those growing in untreated forests in the same location; (4) increasing tree growth (height and diameter) in juvenile ponderosa pines would be associated with greater hydraulic constraints (e.g., reduced hydraulic conductivity due to increased water demand for tissue maintenance), potentially reflected by increased hydraulic vulnerability in larger trees; and (5) site-specific soil properties would influence the physiological drought response of juvenile ponderosa pines, leading to variation in their vulnerability to xylem embolism across locations.

Materials and methods

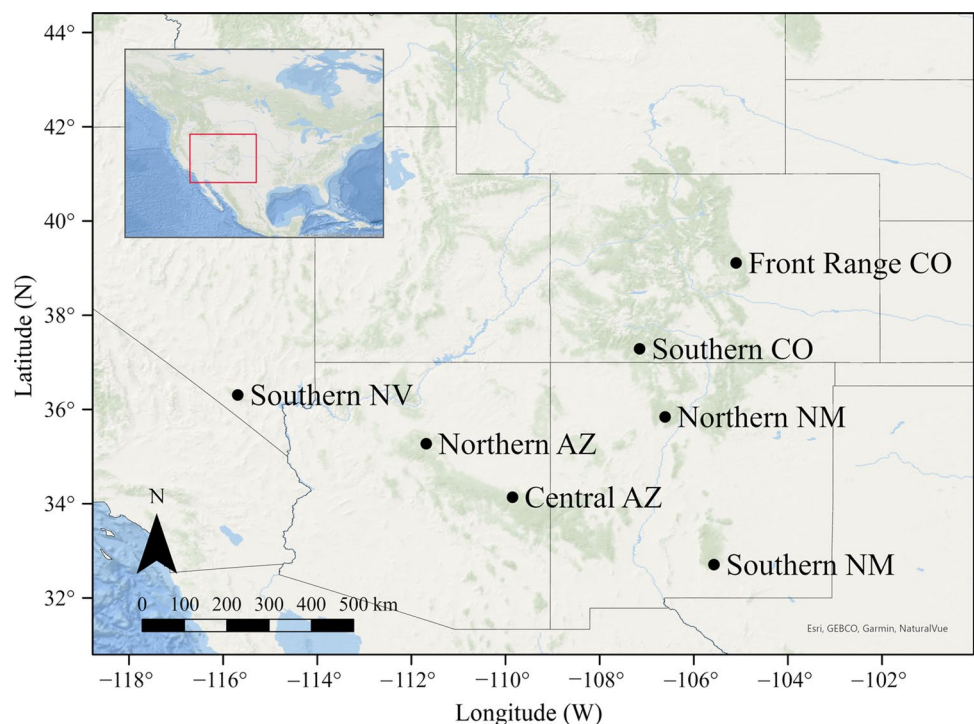
Study area and stand characteristics

The research was conducted in ponderosa pine-dominated forests in eight regional locations across the SWUS, Arizona (AZ), Colorado (CO), New Mexico (NM) and Nevada (NV) (Fig. 1). The selected sites were dominated by Rocky Mountain ponderosa pine (*Pinus ponderosa* var. *scopulorum*

Engelm.). At one site in southern Nevada, ponderosa pine co-dominated with white fir (*Abies concolor*) and Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca*). For the characterization of the climate regime of each site, daily meteorological estimates from 1990 to 2020 were used at 1.0 km² resolution from Daymet (Thornton et al. 2022; <https://daymet.ornl.gov/>). There was substantial variation in annual climate conditions between study locations, as well as during the growing (April–September) and dormant season (October–March) (Tables S1 and S2). Southern CO experienced the highest total annual precipitation, of which 53% occurred during the dormant season. Front Range CO, northern CO and southern NV experienced the lowest annual precipitation, with the majority occurring during the growing season for Front Range CO (72%) and northern CO (62%). For southern NV, the majority of precipitation occurred during the dormant season (69%). Northern AZ, central AZ, southern NM and northern NM experienced intermediate year-round precipitation totals with monsoonal growing season precipitation dominating (53% to 68%), with the exception of northern AZ which had equally distributed precipitation between seasons. Locations at more southern latitudes (central AZ and southern NM) had warmer air temperatures than locations at more northern latitudes (northern AZ, northern NM, southern NV, southern CO, Front Range CO and northern CO).

Ponderosa pine P50 values from two separate field-collected datasets were utilized in this study. Dataset 1 included P50 values of adult and juvenile ponderosa pines

Fig. 1 Ponderosa pine study locations in the southwestern US. For clarity, locations throughout the text are abbreviated as: NCO (northern Colorado), FCO (Front Range Colorado), SCO (southern Colorado), SNV (southern Nevada), NAZ (northern Arizona), CAZ (central Arizona), NNM (northern New Mexico) and SNM (southern New Mexico)



from three locations: northern AZ (35.280° N, 111.721° W), Front Range CO (39.126° N, 105.114° W) and northern CO (40.763° N, 105.613° W). These locations included closely located adult and juvenile trees, which was ideal for our adult-juvenile analysis, but the dataset did not include field characterization of the sampling sites. Dataset 2 included P50 values of juvenile ponderosa pines across six sites in Arizona, New Mexico, Nevada and Colorado (refer to Table S3 for geographic coordinates), also included a detailed characterization of topographic, biometric and compositional characteristics, and near-surface (0–10 cm depth) soil properties (described in Pirtel et al. (2021) and Petrie et al. (2023); Tables S3 to S5). Dataset 1 was employed to compare P50 values, to allude to potential differences in the hydraulic stress tolerance of adult versus juvenile ponderosa pines. Dataset 2 was used for a more in-depth analysis of juvenile hydraulic stress tolerance across climatically diverse locations. Datasets were not combined in our analyses.

Using the sampling methodology of Pirtel et al. (2021), 12 circular plots were selected across six locations for Dataset 2. The plot radii ranged from 5 to 20 m, depending on the juvenile tree density. Plots were located at similar elevations within the range of 2219–2601 m and on shallow slopes, when feasible less than 10° (Table S3). The average ground-line diameter (GLD) of sampled juvenile trees was 45 ± 16 mm, and their average height was 1314 ± 480 mm (Table S4). None of the juvenile sampling sites experienced stand-replacing disturbance or widespread mortality in the last 50 years or more from either human management or natural causes. Sampling included both unmanaged forest sites (N: experiencing no management treatments in the past ~30 years or more) and managed sites that experienced a variety of treatments, including basal area reduction (T), understory thinning and debris removal (U), controlled understory burning (B) and mowing (M; Table S4). Management types were determined by consulting forest managers. All managed sites were treated on dates occurring subsequent to germination of our sample juveniles. Soil texture classes across sampling locations were loam, silt loam and clay loam. Soil organic matter content varied significantly between 3 to 12%, and pH ranged between 6 and 8 (Table S5).

Field sampling and laboratory analysis

Field work was conducted in summer 2021. We did not measure the hydraulic vulnerability of ponderosa pine seedlings (<5 years old) due to their small size, time constraints and lack of suitable equipment for laboratory analysis of small seedling branches. However, comparing the hydraulic vulnerability of juveniles (>20 years old) to mature adults can provide insight on how the hydraulic stress tolerance of ponderosa pines differs at earlier stages of development. The first dataset included 77 juvenile and adult ponderosa pine branches sampled from three SWUS locations (Table 1). This dataset provided P50 values for 69 trees (33 adults and 36 juveniles). For the second dataset, 176 juvenile ponderosa pine branches from 12 plots in six SWUS locations were sampled in the field and provided P50 values for 110 juvenile trees (Table 2). Although the exact age of juvenile ponderosa pines was not determined, general height and diameter relationships with tree ring count developed by Pirtel et al. (2021) suggested that all juveniles were older than 20 years. Adult ponderosa pines were all >50 years in age. Adult and juvenile ponderosa pine branches were collected in the field using a pruning tool and ranged in diameter from 3 to 10 mm. No influence was expected from our branch diameter range with P50 values, as evidenced by Johnson and Brodribb (2023). Adult tree branches were collected from the lower canopy (approximately 5–6 m high) on the south side of the tree. The branches were cut at both ends to a length of 20 cm while submerged in distilled water, wrapped in a damp paper towel and sealed in a plastic bag. Samples were shipped on dry ice overnight to the USDA Forest Service, Rocky Mountain Research Station in Fort Collins, Colorado, where they were stored in a cold room at 2 °C.

The branches in the laboratory were shortened to 14 cm length while submerged in distilled water, and 1.5 cm of bark at both ends was removed. The barked portion of the branch segment was then sealed with adhesive and polytetrafluoroethylene (PTFE) film tape and wrapped in a wet paper towel to prevent drying during the analysis. Samples were flushed following the methodology described in Hietz et al. (2008) and Rosner et al. (2019). This ensured the same initial state

Table 1 Summary of the number of branches sampled, usable samples that provided data in the laboratory analysis, mean P50 $\pm$ standard deviation and mean branch sample diameter $\pm$ standard deviation across study sites in Dataset 1

Location	Tree age stage	Field samples	Usable samples	Mean P50 (MPa)	Mean branch diameter (mm)
NAZ	Adult	12	11	-4.0 ± 0.6	9.0 ± 0.9
	Juvenile	14	13	-4.3 ± 0.6	8.7 ± 1.2
FCO	Adult	18	17	-3.6 ± 0.8	6.2 ± 0.8
	Juvenile	14	13	-4.2 ± 0.8	5.3 ± 0.9
NCO	Adult	7	5	-3.2 ± 0.4	6.6 ± 1.0
	Juvenile	12	10	-6.0 ± 2.2	7.7 ± 1.4

Table 2 Summary of the number of branches sampled, usable samples that provided data in the laboratory analysis, mean P50 $\pm$ standard deviation values and mean branch sample diameter $\pm$ standard deviation across study sites in Dataset 2

Location	Plot ID	Management type	Field samples	Usable samples	Mean P50 (MPa)	Mean branch diameter (mm)
NAZ	1	TB	24	17	-4.5 ± 0.7	5.7 ± 0.8
CAZ	2	TB	12	10	-4.1 ± 1.1	4.8 ± 0.7
	3	TU	12	5	-4.0 ± 0.7	4.8 ± 1.0
SNM	4	N	12	9	-3.7 ± 1.1	4.7 ± 1.0
	5	TU	12	8	-3.7 ± 0.6	4.6 ± 0.7
NNM	6	N	12	7	-4.2 ± 0.5	5.6 ± 1.7
	7	TU	16	7	-5.0 ± 0.5	5.2 ± 0.8
SCO	8	TU	16	12	-4.2 ± 0.6	5.8 ± 1.2
	9	TBM	16	11	-4.4 ± 1.0	5.9 ± 1.5
SNV	10	N	16	8	-4.1 ± 0.9	5.3 ± 0.4
	11	N	12	11	-5.9 ± 0.8	8.8 ± 1.5
	12	TU	16	5	-4.6 ± 0.8	4.6 ± 1.1

In the management type column: N denotes no management in the past ~30 years or more, T stand thinning/basal area reduction, U understory thinning and debris removal, B understory controlled burning and M understory mowing

for all branch samples prior to taking conductivity measurements. After flushing, the flow rate of the branch segment was measured, which is the flow lacking an influence of pressure. Thereafter, the pressurized flow was measured by inducing a hydraulic head on the branch segment using an elevated IV bag filled with distilled and degassed water. After repeating the background measurements, the branch was removed from the apparatus. The hydraulic vulnerability was measured using the centrifugation method (Alder et al. 1997). This method was preferred over others such as bench dehydration (Sperry and Tyree 1988) or air injection (Cochard et al. 1992) due to the ability to quickly process large numbers of samples. The hydraulic conductance of each branch segment was measured using a specialized rotor attached to a centrifuge (Du Pont Sorvall RC-5B) by fitting branch segments into the rotor and placing the exposed ends in reservoirs of filtered water. Thereafter, the centrifuge was spun at increasing angular velocities to induce more negative pressures (0.5 MPa increments) until complete emboli were propagated. For recording and calculating the conductance measurements from an electronic balance, the R-package conductoR was used (Bacher 2022). The R-package fitplc was then used to generate percent loss values, fit vulnerability curves (the relationship between the relative percent loss of hydraulic conductivity and xylem water stress; Sperry and Tyree 1988) and to predict P50 with confidence intervals using non-parametric bootstrap (Duursma and Choat 2017; vulnerability curves presented in Figs. S1 and S2). While other drought tolerance measures exist, such as P12 (the pressure causing 12% loss, approximating the initiation of embolism) and P88 (the pressure at full embolism), P50 is the most widely used measure in plant hydraulic studies. In the first dataset of the 77 sampled branches (37 adults and 40 juveniles), 69 (90%) provided usable data (33 adults

and 36 juveniles; Table 1). In the second dataset, 110 of 176 juvenile branches (63%) yielded usable data (Table 2). Sample errors were caused by irreparable embolization of branch conduits, excessive resin-blocking flow through the xylem, and conductance irregularities that prevented accurate measurement.

SOILWAT2 water balance simulations

Water balance and temperature characteristics of the juvenile sampling sites (Dataset 2) were simulated using the SOILWAT2 ecosystem water balance model. SOILWAT2 is a point-based, process model that simulates soil water pools and fluxes across multiple soil layers as a function of the soil–plant–atmosphere interactions by incorporating the Penman energy-balance evapotranspiration estimates (Schlaepfer and Murphy 2023). SOILWAT2 has, in recent years, been successfully used to simulate the water balance and temperature dynamics of forests in the SWUS, including comparison of treated and untreated forest stands (Andrews et al. 2020; Petrie et al. 2020, 2023; Bradford et al. 2022). The model was parametrized using characterization data for each sampling site, including topography, slope and aspect, forest density and overstory attributes, and understory vegetation, litter and debris (Tables S3 and S4). Site-specific soil properties were parametrized in the model using soil texture percentages calculated from near-surface (0–10 cm) soil samples (Table S5). Sub-surface (> 10 cm) soil properties were derived from POLARIS (Chaney et al. 2019) and probabilistic soil property databases (Miller and White 1998; Table S6).

SOILWAT2 simulations were conducted for each study site, at the daily time step, for the 1990–2020 water years. The model was forced using Oak Ridge National Laboratory

DayMet estimates of daily precipitation and air temperature at 1 km² resolution (Thornton et al. 2022; <https://daymet.ornl.gov/>). Monthly means of relative humidity, wind speed and cloud cover were integrated into the daily simulations, and were obtained from the Climate Maps of the United States (NCEI 2023). The SOILWAT2 model was used to simulate soil hydraulic properties and daily potential evapotranspiration at each site (Table S7). The R-package rSOILWAT2 v6.0.2 was used to run simulations (Schlaepfer and Murphy 2023).

Analyses

Our analyses focused on both meteorological estimates and water balance simulations at each study site during the April–September growing season when juvenile trees are active and most likely to experience water stress. Meteorological estimates included precipitation amounts (P ; mm), air temperatures (T ; °C) and potential evapotranspiration (ET_p ; mm), as well as derived variables such as the aridity index (AI) and growing degree days (GDD ; °C). AI is the ratio of potential evapotranspiration (ET_p ; mm) to precipitation (P ; mm) (Eq. 1), whereas the growing degree days (GDD ; °C) is calculated by subtracting a base threshold temperature (T_{base} ; °C) from the average daily air temperature (°C) (Eq. 2). The GDD were determined using a 10 °C base threshold.

$$AI = \frac{ET_p}{P} \quad (1)$$

$$GDD = \frac{T_{max} + T_{min}}{2} - T_{base} \quad (2)$$

Our analyses of water balance focused on soil depths within the juvenile ponderosa pine rooting zone (0–20 and 20–50 cm). The exception was southern Nevada which had a restrictive soil feature below 40 cm, and we simulated and evaluated soil water balance from 0–20 and 20–40 cm for these sites (Table S6). Water balance simulations included soil volumetric water content (VWC ; m³ m⁻³), soil water potential (SWP ; MPa) and soil water availability (SWA : total mm of extractable water in above a soil water potential of –3.0 MPa).

Statistical analysis

Yuen's test was used to examine statistical differences in P50 values between adults and juveniles, as well as between management treatments within each location. One-way robust ANOVA was used to examine significant differences in P50 values, seasonal climate and soil–water variables between locations. If the ANOVA was significant, the linear contrasts

method was employed as a *post-hoc*-test reporting adjusted P -values, given multiple comparisons in trimmed means to determine which groups were significantly different from each other. Both tests have shown to have high statistical power and do not require the assumptions of normality and homogeneity of variance (Mair and Wilcox 2020). Robust statistical analyses were conducted using the R-package WRS2 (Mair and Wilcox 2020). Simple linear regression analyses were performed to evaluate the relationship between P50 values with environmental and morphological characteristics of the forest plots. Statistical significance was set at $P < 0.05$. To quantify probability distribution similarities between P50 values across locations in the SWUS, the distribution-free overlapping index (η) was calculated using the R-package overlapping (Pastore 2018). The overlapping index ranges from 0 to 1, with 0 indicating that distributions are completely separated and 1 indicating that distributions are identical. The use of the overlapping index minimizes the potential for biased results attributable to outliers. P50 values which do not overlap, in terms of their density functions, are considered significantly different.

Results

Ponderosa pine hydraulic vulnerability

Overall, juvenile ponderosa pines exhibited significantly greater branch resistance to xylem embolism than adult trees (i.e., more negative P50 values; Fig. 2a), with pooled mean P50 values of –4.69 MPa and –3.58 MPa, respectively (Dataset 1). However, in northern Arizona, no significant differences were detected in P50 between juvenile and adult trees (Fig. 2b; Table 1), whereas juveniles in Front Range Colorado and northern Colorado displayed significantly higher resistance to xylem embolism compared to adult trees (mean P50 values: –4.20 MPa vs. –3.56 MPa and –5.97 MPa vs. –3.15 MPa, respectively; Fig. 2c, d; Table 1). In Dataset 1, adult ponderosa pines showed significantly lower resistance to xylem embolism with increasing latitude ($R^2 = 0.95$, $P < 0.0001$; Fig. 3a). Conversely, juveniles had increased resistance with increasing latitude ($R^2 = 0.53$, $P < 0.0001$). Though not significant, Dataset 2 also suggests a latitude-dependent trend in juvenile P50 values, with potentially more negative values (greater vulnerability) at higher latitudes (Fig. S3).

In our comparison of juvenile trees only (Dataset 2), juveniles in southern Nevada (mean = –5.05 MPa) and northern New Mexico (mean = –4.63 MPa) presented significantly higher resistance to xylem embolism than juveniles in southern New Mexico (mean = –3.72 MPa; Fig. 3b; Table 2). The xylem specific hydraulic conductivity (K_s) was predictive of the vulnerability to xylem embolism (P50) for pooled data of

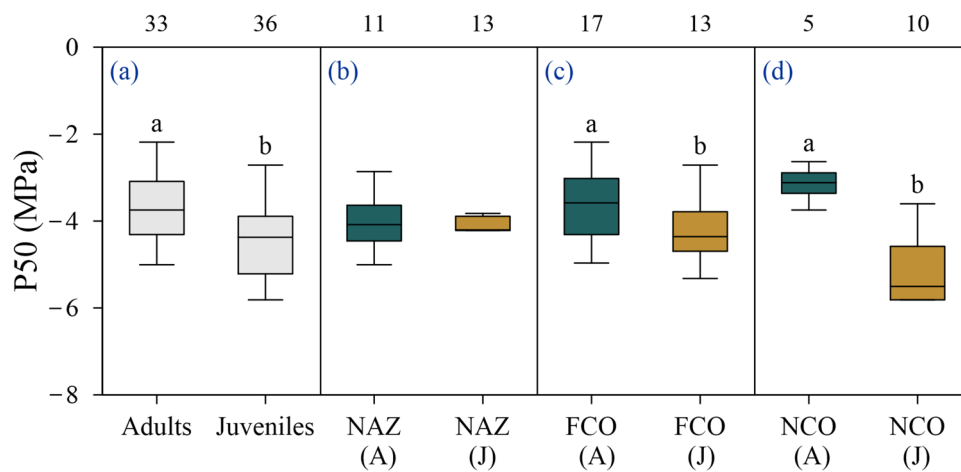


Fig. 2 Boxplot of pooled P50 values for: **a** adult and juvenile ponderosa pines; **b** adults and juveniles in northern Arizona; **c** adults and juveniles in Front Range Colorado; and **d** adults and juveniles in northern Colorado. Locations are ordered from lowest to highest latitude. Each box plot shows the median (center line), the interquar-

tile range (25%–75%), and the lower and upper quartile range (0–25% and 75%–100%) multiple to a factor of 1.5 (whiskers). Outliers are not shown. Letters indicate significant differences at $P < 0.05$ (using the Yuen test). Numbers above each boxplot refers to the number of observations. In panels **b–d**, A denotes adults and J denotes juveniles

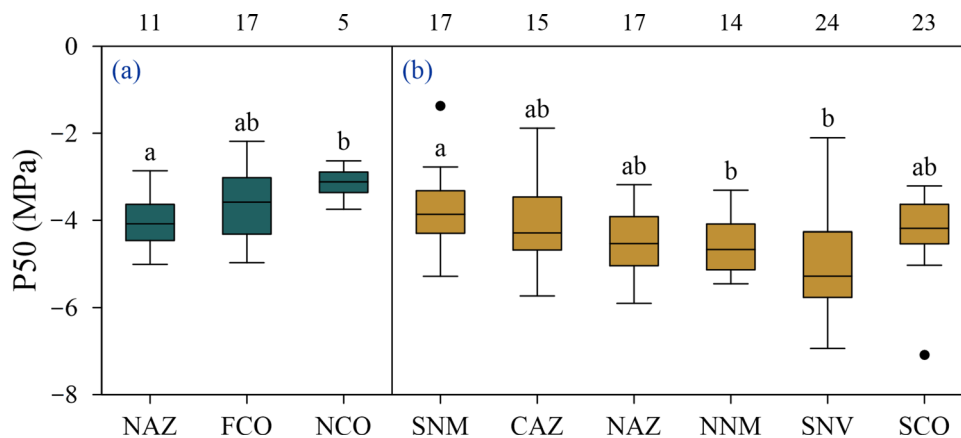


Fig. 3 Boxplot of pooled P50 values for: **a** adult ponderosa pines by location (Dataset 1); and **b** juvenile ponderosa pines by location (Dataset 2). Locations are ordered from lowest to highest latitude. Each boxplot shows the median (center line), the interquartile range (25%–75%), and the lower and upper quartile range (0–25% and

75%–100%) multiple to a factor of 1.5 (whiskers). Dots represent outliers. Letters indicate significant differences at $P < 0.05$ (evaluated using robust ANOVA and linear contrasts *post-hoc*). The number above each boxplot refers to the number of observations

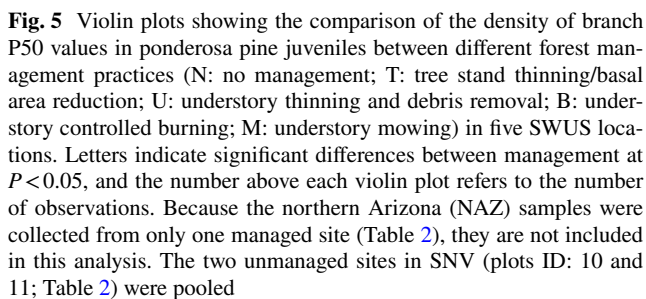
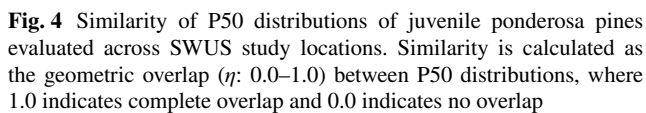
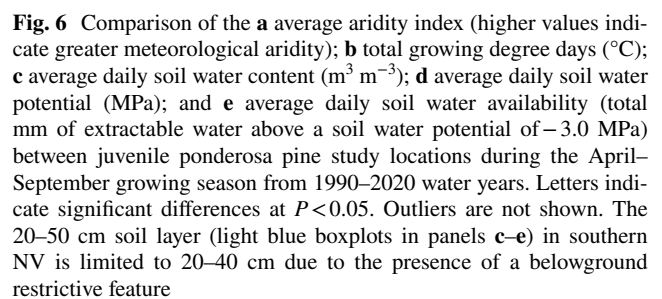
juvenile ponderosa pine (Fig. S4; $P < 0.0001$, $R^2 = 0.18$). K_s was negatively correlated with P50, such that increased K_s corresponded to a decreased (i.e., more negative) P50. Probability distributions of juvenile P50 values across SWUS locations were highly similar, based on the overlap index of their area under the curve ($\eta > 0.5$; Fig. 4). However, the overlap between SNM–NNM, SNV–SNM and SCO–SNV had the lowest similarity in distribution ($\eta = 0.5$), which was consistent with significant P50 differences observed between these locations (Fig. 3).

With the exception of northern NM, no significant differences were found in the P50 values of juvenile ponderosa pines

growing on sites with different management types (Fig. 5). In northern NM, the forest plot with overstory and understory management showed a mean P50 of -5.0 MPa, compared with the unmanaged plot with -4.2 MPa. This significant difference was not observed in southern NM and southern NV, which had the same management types as northern NM.

Climate and soil water conditions across the study sites in the SWUS

The aridity index was significantly higher in southern Nevada compared to other locations (Fig. 6a), due to its low

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feature at 40 cm depth; Fig. 6c–e). Overall, VWC, SWP and SWA at 0–20 cm were significantly higher in northern New Mexico and southern Colorado compared to other locations (Fig. 6c–e). In the 20–50 cm layer, lower VWC was observed in northern New Mexico, while lower SWP occurred in northern New Mexico and southern Colorado (Fig. 6c, d; Table S7). Conversely, there was lower SWA was detected in Arizona locations (Fig. 6e; Table S7). Across both soil layers, northern New Mexico had fewer growing season days with no SWA, and had fewer days with SWP lower than the site-specific mean P50 value compared to southern New

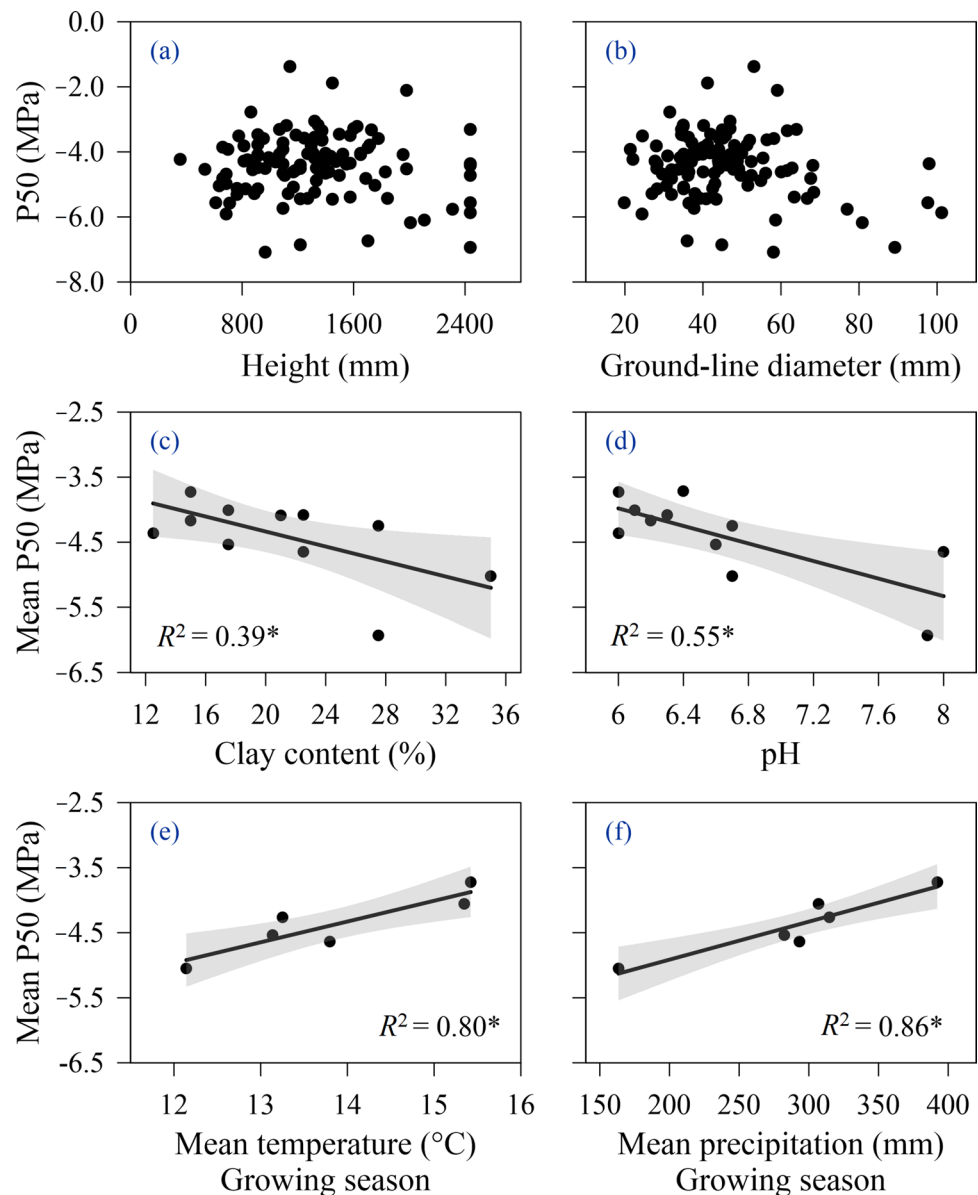
Mexico and southern Nevada (Table S8). In contrast, southern Nevada had a greater number of days with no SWA, a similar number of days with low SWP values at the 0–20 cm layer, and significantly fewer days at the 0–50 cm layer compared to southern New Mexico (Table S8).

Climatic, edaphic and tree growth factors broadly associated with juvenile P50

There were no significant relationships between P50 values of juvenile ponderosa pines and their individual height or their ground-line diameter (Fig. 7a, b). Statistically significant negative linear relationships were found between

the mean P50 of juvenile ponderosa pines and soil clay content at a 0–10 cm depth, as well as pH at 0–10 cm depth (Fig. 7c, d). Statistically significant positive linear relationships between mean P50 and mean daily growing season temperature, and between mean P50 and mean total growing season precipitation were found at our study locations (sites pooled) (Fig. 7e, f). These results correspond with regional climate variation in the SWUS, where higher precipitation forest locations during the growing season have warmer temperatures, and lower precipitation locations have cooler temperatures (Fig. S5). There was no significant relationship between P50 values of juvenile ponderosa pines and understory vegetation cover, aridity index or soil hydraulic properties (Fig. S6).

Fig. 7 Relationships between P50 values of juvenile trees and **a** individual tree height (mm); and **b** individual tree ground-line diameter (mm). Relationships between pooled mean P50 values of juvenile trees and **c** soil clay content at 0–10 cm depth (texture %); **d** soil pH at 0–10 cm depth; **e** mean daily growing season temperature (°C; 1990–2020 water years); and **f** mean total growing season precipitation (mm; 1990–2020 water years). In panels **c**, **d**, P50 values were pooled by plot, whereas in panels **e** and **f**, P50 values were pooled by location. The shaded gray area indicates the 95% confidence interval, and asterisks indicate statistical significance using linear correlation ($P < 0.05$)



Discussion

Variation in adult and juvenile hydraulic vulnerability

As conifers grow older, a trade-off between optimal hydraulic supply to the existing leaf area and the maintenance costs of supporting xylem tissue leads to reduced water transport efficiency (Mencuccini 2002; McDowell and Allen 2015). This inefficiency might be linked to more negative P50 values. However, Domec et al. (2009) found no significant differences in the branch P50 values of adult versus juvenile ponderosa pines. More broadly, similar results have been reported for other tree species (Matzner et al. 2001; Lucani et al. 2019). Contrary to our expectations, branch P50 data from three SWUS locations in Arizona and Colorado show that at two of these locations, juvenile ponderosa pines were on average less vulnerable to xylem embolism than adult trees. Our results suggest that hydraulic vulnerability in ponderosa pine may be lower at earlier stages of development (i.e., greater hydraulic stress tolerance), such that future drought stress imposed by climate change may have effects that differ between trees at different developmental stages. Due to their shallow root system (Pirtel et al. 2021), developing juveniles may rely on shallow soil moisture for over a decade before reaching deeper, more consistent water sources; greater resistance to xylem embolism could be crucial for their survival. While our findings are limited by a small number of locations studied, a broader analysis across a greater number of regional environments and forest settings would help to further elucidate our findings.

Our results show moderate variability in P50 values across juvenile ponderosa pine populations, ranging from -3.7 MPa in southern NM to -5.0 MPa in southern NV. This variability indicates that juveniles in southern NV, the most water limited location of our study, were 1.4 times less vulnerable to xylem embolism compared to juveniles in southern NM. This result is bolstered by our pooled branch mean P50 of -4.4 MPa ($n = 110$) for juvenile ponderosa pines, which aligns with the branch mean P50 of -4.6 MPa ($n = 10$) reported by Domec and Pruyn (2008) for the Cascade Range of Oregon.

Climate influence in adult and juvenile hydraulic vulnerability

A number of studies have found no significant differences in P50 between adult ponderosa pine populations in contrasting climates and habitats (Maherali and DeLucia 2000; Bouffier et al. 2003; Stout and Sala 2003). Recent research suggests that regeneration failure in ponderosa pine forests was more common at lower latitudes in the SWUS (Davis et al. 2023; Petrie et al. 2023). Ponderosa pine in the SWUS exhibits a latitudinal pattern of genetic variation (i.e., morphological

and developmental traits) in growth potential, with significant differences observed along a north–south gradient (Rehfeldt 1993; Rehfeldt et al. 2014). It is therefore appealing to ascribe a latitudinal framework to the hydraulic vulnerability of ponderosa pines, and postulate that regional variation in adult and juvenile P50 values is associated with regional climate variation across latitudes. We found that adult ponderosa pines had less negative P50 values at higher latitudes, which were associated with a decrease in growing season temperatures (Table S2), consistent with Jiang et al. (2021). This suggests that higher temperatures may be related to higher vapor pressure deficit (VPD) and higher transpiration rates, which boosts water stress. On the other hand, juveniles showed more negative P50 values at higher latitudes and were associated with higher growing season temperatures and precipitation. These results contradict findings by Li et al. (2018), who identified a negative relationship between mean annual precipitation and P50, and He et al. (2020), who found a positive correlation between growing season temperatures and precipitation and xylem specific hydraulic conductivity (K_s). However, in our study, K_s was weakly negatively correlated with P50 (Fig. S4). Our results suggest that juvenile populations with higher growth potential (Rehfeldt 1993; Rehfeldt et al. 2014) may also have increased tolerance to drought stress. Although we detected low variability in the hydraulic vulnerability trait between juvenile populations (Fig. 4), southern NM–southern NV, southern NM–northern NM and southern CO–southern NV locations had relatively dissimilar distributions of P50 values. Despite the greater exposure to water stress (Table S8), southern NM exhibited a less negative P50 value compared to northern NM, which supports the idea that hydraulic vulnerability in southern NM is not solely determined by environmental factors. These findings suggest that southern NM, northern NM and southern NV populations may possess genetic or phenotypic variations (Maherali et al. 2002; Kolb et al. 2016; Wu et al. 2023).

Over long timescales, tree hydraulics adapt to climate variability, enabling trees to cope with aridity and temperature stress (Vicente et al. 2022). We did not observe a safety versus efficiency trade-off in ponderosa pine (Fig. S4), consistent with Kilgore et al. (2020). This is a counterintuitive finding, as studies in other species have found a trade-off between efficiency and tolerance (van der Sande et al. 2019). However, a global study by Liu et al. (2021) found weak evidence for a hydraulic trade-off between efficiency and safety. Therefore, ponderosa pine juveniles may decrease their hydraulic efficiency in locations with greater water availability, potentially at the expense of xylem embolism tolerance, leading to regional variation in hydraulic vulnerability that is organized across wetter and drier locations. Recent research in other species has shown less negative P50 values for trees with higher soil water availability

(Weithmann et al. 2022) and lower aridity index (Stojnić et al. 2018), which agrees with our findings. However, it does not mean that ponderosa pine forests in drier habitats are immune to drought stress. Although growing season precipitation and temperatures are positively correlated across the SWUS, we recognize the lack of a definitive explanation for our observation of a positive P50 relationship with average growing season temperature but hypothesize a possible explanation for further investigation. Evidence suggests that ponderosa pines exhibit an adaptive reduction in tracheid diameter, either related to genetic variation or phenotypic plasticity in montane sites compared to warmer desert sites (Maherali and DeLucia 2000), as well as in other conifers at colder temperatures where it serves as a protective mechanism against freezing-induced embolism (Pittermann and Sperry 2006). In conifers, narrower conduits are associated with greater xylem embolism tolerance (Sperry et al. 2006), which may explain the more negative P50 values at lower temperatures in southern NV and less negative values at greater temperatures in southern NM. However, Bouche et al. (2014) found that increased embolism resistance in conifers might not necessarily come at the cost of narrower tracheid diameters and should therefore have a minor impact on hydraulic efficiency. The relationship between xylem conduit diameter and P50 remains a topic of debate (Anfodillo and Olson 2021). Further research is needed to elucidate this connection in juvenile ponderosa pines.

Influence of soil properties on ponderosa pine hydraulic vulnerability

If the hydraulic stress tolerance of juvenile ponderosa pines is a plastic trait, it follows that management treatments that modify stand temperatures and soil water availability (Feeney et al. 1998; Hardage et al. 2022; Sankey and Tatum 2022) may also modify tree stress tolerance. We did not observe significant differences in juvenile P50 between management treatments in our study sites, although we note that our managed sites were treated after our sample juvenile trees had germinated and established. In northern NM we found greater juvenile hydraulic vulnerability in unmanaged versus managed sites, but caution that sample trees in the unmanaged site were growing at exceptionally high density (est. > 5.0 ind. m^{-2}), such that this difference may be more attributable to competitive stress than to management influence (Wu et al. 2023). We recommend that the development of clear relationships between juvenile stress tolerance and management treatments will require long-term studies initiated in managed and unmanaged stands prior to seedling establishment.

Research has sought to attribute variation in physical and chemical soil properties to germination and establishment of ponderosa pine (Howell 1932; Puhlick et al. 2021; Petrie

et al. 2023), and often reported difficulty in doing so. Yet, establishing connections between soil properties and hydraulic vulnerability may be a key component of understanding environmental control on regeneration. Precipitation regimes and soil parent material influence soil pH, with alkaline soils prevailing in drier climates (Slessarev et al. 2016; Puhlick et al. 2021). Our observation of a negative relationship between soil pH and P50 values (more negative P50 with more alkaline soils) may reflect an interrelationship between regional meteorology and soil chemistry. Supporting these findings, Secchi et al. (2023) demonstrated that alkaline soil conditions influence plant hydraulics through physiological and chemical adjustments that aid in drought tolerance. On the other hand, Howell (1932) demonstrated that survival and growth rates of ponderosa pine are related to soil texture. We found a negative relationship between soil clay content in the shallow soil layer (0–10 cm depth) and P50 values. Although soil clay content and water holding capacity are positively correlated (Bordoloi et al. 2019), we postulate that the very high surface clay content that we observed for sites with more negative P50 values may indicate a severe decline in soil hydraulic conductivity holding more moisture at the surface soil layer, increasing evaporation and thus amplifying soil water stress (Jarvis et al. 2013). Our results corroborate those of Hacke et al. (2000), and Sperry and Hacke (2002), which report more negative P50 in vegetation growing on finer textured soils, but contrast the results of Hultine et al. (2006), which reports no significant difference.

Tree development and adaptation versus acclimation of hydraulic vulnerability to local environmental stress

Recent research has postulated that the tree development is linked to hydraulic vulnerability, such that hydraulic efficiency takes precedence over hydraulic stress tolerance (e.g., limitation of embolism) as tree height increases (Prendin et al. 2018), i.e. hydraulic vulnerability increases as trees grow larger. Examination of global databases reveals that taller trees exhibit less negative P50 (Liu et al. 2019) and higher mortality rates during drought events (Bennett et al. 2015). Conversely, Fernandez-de-Uña et al. (2023) demonstrated that taller conifer trees exhibit more negative P50, effectively mitigating species and site confounding effects as compared to Liu et al. (2019). Contrary to our initial expectations, we found no discernible correlation between P50 values and juvenile height or diameter. It is likely that the evaluated tree size range (about 2 m in height and 8 cm in diameter) is not sufficient to observe contrasting differences in hydraulic vulnerability.

Interestingly, Vaughan et al. (2019) demonstrated that ponderosa pine wood density increases during drought, and a growing body of evidence suggests that increasing wood density may be associated with reduced vulnerability to

embolism in ponderosa pine (Bouffier et al. 2003; Domec et al. 2009) and other species (Rosner 2017; Savi et al. 2019). Therefore, we postulate that juveniles in southern NV (the most water limited location of our study) may exhibit high embolism resistance via growing denser wood/narrower xylem conduits. In total, our result suggests that all 3 factors: regional climate variation, soil properties and population acclimation and/or adaptation show signs of influencing the hydraulic vulnerability of ponderosa pine juveniles in the SWUS. Disentangling where and to what degree these different factors are influential is likely to be a crucial component of determining the sensitivity of ponderosa pine forests in this region to a more water limited future.

Conclusion

We investigated the variability of hydraulic vulnerability in ponderosa pine populations across climatically diverse locations in the SWUS, presenting the first comprehensive dataset for juvenile pines in the region. Juvenile ponderosa pines exhibited lower hydraulic vulnerability than mature adult trees, suggesting that hydraulic vulnerability varies between these developmental stages. This finding underscores the importance of incorporating species stress tolerance at different developmental stages to inform regional, whole-ecosystem responses to climate change. Juvenile ponderosa pines in southern Nevada displayed more negative P50 values than those of some study locations, which was attributable to greater climate stress and water limitation. In contrast, differences between southern and northern NM were less attributable to abiotic factors, and may allude to the potential for trait variation between populations. Latitudinal gradients in growing season precipitation and temperature across the SWUS were associated with variation in the hydraulic vulnerability of both adult and juvenile ponderosa pines. Although we found no evidence that forest management practices or tree size were associated with the hydraulic vulnerability of juvenile ponderosa pines, soil properties, specifically pH and clay content, might play an important role in mediating how climate impacts their stress tolerance. The high similarity in xylem embolism tolerance distribution that we observed across the majority of our SWUS study locations could pose a significant constraint on the persistence of ponderosa pine populations in a warmer and drier future by restricting tree survival at early developmental stages. Future research on hydraulic vulnerability in this species would benefit from the coupling of genetic and phenotypic analyses, sampling of naturally grown individuals, and evaluation of local climate and forest conditions to determine if stress tolerance is inherent or a result of abiotic controls.

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