SEASONAL CLIMATE AND ENVIRONMENTAL CONDITIONS ASSOCIATED WITH PHYSIOLOGIC VARIATION OF SOUTHWESTERN UNITED STATES PINES

By

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ABSTRACT

Juvenile and adult conifers in the southwestern United States are vulnerable to a range of different abiotic and biotic factors, yet it is unclear how their stress tolerance varies across environments. Predicted increases in the frequency and intensity of disturbance as well as greater climate and weather variability across the region highlight the potential for differential physiological responses across tree species and populations. This thesis focuses on two physiologic mechanisms, hydraulic vulnerability and mortality, that could be altered by climate change in two broadly distributed southwestern United States conifers: ponderosa pine and pinyon pine.

In chapter 2, I measured the hydraulic vulnerability of juvenile (∼20-30 years old) ponderosa pines (*Pinus ponderosa*) in six climatically-varying locations (northern and central Arizona, southern and northern New Mexico, southern Colorado, and southern Nevada) of the southwestern United States (SWUS). I evaluated hydraulic vulnerability using the p50 value of stem conduits. P50 is the pressure (MPa) at which 50% of xylem conductance is lost, and lower p50 values correspond to lower tree vulnerability to soil moisture limitation. I then contrasted the climate and environmental conditions of our sampling sites from 1990-2020 using site characterization data, gridded meteorological estimates (DayMet), soil estimates (POLARIS), and soil water balance modeling (SOILWAT2). My objectives were to determine if hydraulic vulnerability varied between juvenile ponderosa pines growing in different subregional locations, and to determine if climate and environmental variables were associated with these differences. Juvenile ponderosa pines in southern Nevada had more negative p50 values (-5.05 ± 1.16 MPa) than juveniles in southern Colorado

(-4.26 ± 0.79 MPa), southern New Mexico (-3.72 ± 0.86 MPa), and central Arizona (-4.06 ± 0.96 MPa; ANOVA, $p < 0.05$). Compared to all other SWUS locations, southern Nevada also had significantly more severe warm season (April-September) meteorological moisture deficit, lower cool season (October-March) and warm season soil water potential [ψ_p: MPa], and lower soil water holding capacity ($p < 0.05$). Thus, lower ψ_p, imparted by low warm season precipitation and physical soil characteristics, was associated with higher stress tolerance found in juvenile ponderosa pines growing in southern Nevada. Although future research is required to determine the reason for their higher stress tolerance – which could include acclimation, adaptation, and/or environmental control – my results provide new evidence for physiological differences at early stages of ponderosa pine development in the SWUS.

In chapter 3, I used the Cox Proportional Hazards (PH) model to evaluate background mortality hazard for adult pinyon pines in three climatically-varying locations (Colorado, Arizona, and Nevada) of the southwestern United States (SWUS). Life status (living/dead) and tree size were recorded for *Pinus edulis* (Colorado pinyon; Colorado, Arizona) and *Pinus monophylla* (singleleaf pinyon; Nevada) over multiple 10-year periods from 2001-2019 (USFS FIA). I then contrasted the climate and environmental conditions of each location using gridded meteorological estimates (DayMet) and soil simulations (POLARIS). My objectives were to determine if background mortality varied between adult pinyon pines growing in different sub-regional locations over a 10-year period, and to analyze associated variables and their potential time-dependent effects for *P. edulis* and *P. monophylla*. 10-year background mortality ranged from 4-6% across locations and was lower than previously reported for *P. monophylla*. Adult *P. edulis* in Arizona had the greatest cumulative hazard and lowest overall survival probability over a 10-year period. Based on my results, factors influencing background mortality varied between study locations. The probability of

mortality significantly decreased with greater cool and warm season precipitation, % soil organic matter (30-100 cm), and % soil silt content (100-200 cm; $p < 0.05$). The probability of mortality significantly increased with greater tree size (height and diameter), soil pH (30-100 cm), and cool season maximum air temperature ($p < 0.05$). My results show that the mechanisms driving background mortality in adult pinyon pines differ between and among species occupying different climate regimes, and provide further evidence that greater tree size increases the probability of mortality pinyon pine.

ACKNOWLEDGEMENTS

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CHAPTER 1

INTRODUCTION

Semiarid coniferous forests and woodlands of the southwestern United States (SWUS) are home to two widely distributed conifers, ponderosa pine and pinyon pine, that provide a suite of ecosystem services such as maintaining wildlife habitat and generating valuable forest products (Long and Smith, 2000; Romme et al., 2009). Historic and modern climate disturbance have altered the structure and composition of these arid forests (Hicke et al., 2016; Rodman et al., 2022), and forest decline is expected to increase as climate conditions become warmer and drier (Notaro et al., 2012; Shriver et al., 2022). Recent widespread tree mortality and regeneration failures highlight the uncertainty that these forests face, particularly in response to expected climate change. Widespread pinyon pine mortality occurred in the early 2000s due to the occurrence of a prolonged drought event and subsequent insect infestation (Breshears et al., 2008; Gaylord et al., 2013), which resulted in significant loss of forest cover throughout the SWUS region (Clifford et al., 2013; Macalady and Bugmann, 2014). A recent paper by Petrie et al., (2023) found that 29% of sampled ponderosa pine sites across the SWUS experienced regeneration failure. Widespread regeneration failure has also been observed in other conifer species (Hankin et al., 2019; Rammer et al., 2020). These examples highlight the uncertain futures of semiarid confiers in the SWUS, and identify the need to better understand the factors driving significant change in these forest ecosystems.

Climate forecasts indicate that conditions will become more variable and extreme in the SWUS (McKinnon et al., 2021). In the SWUS, precipitation is expected to decrease and temperatures are predicted to increase as the region shifts towards a drier overall climate (Prien et al., 2016). Shifts in the structure and composition of coniferous forests in response to changing climate conditions has already been documented throughout the region (Abella et al., 2015; Hessburg et al., 2019). Climate change is expected to increase the frequency and intensity of disturbances such as drought and wildfire (Wasserman and Mueller, 2023; King et al., 2024), which will have negative impact on regeneration and survival in forest ecosystems (Kemp et al., 2019; Kolb et al., 2020). Also, changes to average climate conditions over time have the potential to influence forest persistence – even in the absence of a major climate event (Taccoen et al., 2021; 2022).

The persistence of semiarid forests and woodlands will depend on how trees respond and ultimately adapt to uncertain climate conditions (Falk et al., 2022). The goal of my two studies was to investigate physiologic variation in conifers growing under contrasting levels of abiotic and biotic stress, and to determine the factors driving these differences across the SWUS region. In chapter 2, I investigated age-related differences of hydraulic vulnerability in *Pinus ponderosa* (ponderosa pine), and explored the climate and environmental factors associated with differences in juvenile *P. ponderosa* hydraulic vulnerability. In chapter 3, I investigated 10-year background mortality risk in two species of pinyon pine in the SWUS, *Pinus edulis* (Colorado pinyon) and *Pinus monophylla* (single-leaf pinyon). I used a survival model to predict the likelihood of adult pinyon pine mortality in response to several factors including meteorology, soil properties, and tree size. The results of my studies highlight how coniferous species in the SWUS might vary in physiological response to contrasting climates due to differences in life history and stand-scale factors. The ability to detect vulnerable or resilient tree populations has implications for forest management (Millar et al., 2007; Williams and Dumroese, 2013) and future research due to the potential for differential responses to predicted climate change across forest ecosystems in the SWUS (Poulos et al., 2012; Whipple et al., 2019).

CHAPTER 2

REGIONAL VARIATION IN HYDRAULIC VULNERABILITY OF JUVENILE PONDEROSA PINES IN THE SOUTHWESTERN UNITED STATES

Chapter abstract: Juvenile ponderosa pines (*Pinus ponderosa*) are vulnerable to water stress imparted by soil moisture limitation and low soil water potentials (ψ_p: MPa), but it is unclear if their tolerance to water stress varies between different environments. We measured the hydraulic vulnerability of juvenile (∼20-30 years old) ponderosa pines in six climatically-varying locations (northern and central Arizona, southern and northern New Mexico, southern Colorado, and southern Nevada) of the southwestern United States (SWUS). We evaluated hydraulic vulnerability using the p50 value of stem conduits. P50 is the pressure (MPa) at which 50% of xylem conductance is lost, and lower p50 values correspond to lower tree vulnerability to soil moisture limitation. We then contrasted the climate and environmental conditions of our sampling sites from 1990-2020 using site characterization data, gridded meteorological estimates (DayMet), soil estimates (POLARIS), and soil water balance modeling (SOILWAT2). Our objectives were to determine if hydraulic vulnerability varied between juvenile ponderosa pines growing in different subregional locations, and to determine if climate and environmental variables were associated with these differences.

Juvenile ponderosa pines in southern Nevada had more negative p50 values (-5.05 ± 1.16 MPa) than juveniles in southern Colorado (-4.26 ± 0.79 MPa), southern New Mexico (-3.72 ± 0.86 MPa), and central Arizona (-4.06 ± 0.96 MPa; ANOVA, $p < 0.05$). Compared to all other SWUS locations, southern Nevada also had significantly more severe warm season (April-September) meteorological

moisture deficit, lower cool season (October-March) and warm season ψ_p, and lower soil water holding capacity ($p < 0.05$). Thus, lower ψ_p, imparted by low warm season precipitation and physical soil characteristics, was associated with higher stress tolerance found in juvenile ponderosa pines growing in southern Nevada. Although future research is required to determine the reason for their higher stress tolerance – which could include acclimation, adaptation, and/or environmental control – our results provide new evidence for physiological differences at early stages of ponderosa pine development in the SWUS.

Taylor E. Brewer was co-author on a variation of this article that is under review in New Phytologist. Contributing authors: Pinos, J. , Hubbard, R. , Frank, J. , Burjoski, V. , Brewer, T. E. , Bradford, J. B. , Schlaepfer, D. , Petrie, M. D.

Variation in the hydraulic vulnerability of juvenile ponderosa pines in the southwestern United States by Pinos, Juan; Hubbard, Robert; Frank, John; Burjoski, Vesper; Brewer, Taylor; Bradford, John B; Schlaepfer, Daniel; Petrie, Matthew (2024; in review).

Introduction

Ponderosa pine forests in the SWUS (southwestern United States) experience a diverse range of cool and warm season climates, environmental conditions, disturbances, and human management (Stephens et al., 2015; O'Connor et al., 2017). Average climate conditions in the SWUS vary across latitudes where southern latitudes characterized by high temperatures and greater warm season precipitation and northern latitudes are typically of milder temperature, dominated by cool season precipitation (Jones and Gutzler, 2016). Variation in seasonal precipitation and temperature across the region may be strongly tied to the North American Monsoon system in the order of years to multiple decades (Adams and Comrie, 1997; Guirguis and Avissar, 2008). Climate conditions can also be influenced by topographic features, elevation, and soil and edaphic properties – leading to considerable environmental variation across ponderosa pine forests (Rodman et al., 2016: Hessburg et al., 2019). In addition to climate-associated differences, ponderosa pine forests have undergone changes in composition and structure due to logging and subsequent fire exclusion beginning in the mid to late-19th century (Covington and Moore, 1994; Hessburg and Agee, 2003). These activities have resulted in greater forest stand densities (Fulé et. al., 1997; 2003; Stephens et al., 2015), higher forest vulnerability to disturbances including drought and insect attack (Negrón and Popp, 2004; Allen et al., 2010; Fettig et al., 2019; Pile et al., 2019), and stand-replacing wildfires (Allen et al., 2002). To improve forest resiliency, land managers in the SWUS have employed interventions including prescribed burning (Cannon et al., 2022; Stoddard et al., 2021) and basal area thinning (Zhang et al., 2013; 2019; Stoddard et al., 2021), often with the goal of replicating historic ponderosa pine stand densities and encouraging natural regeneration.

Natural forest regeneration can be influenced by interactions between climate conditions, topography, and forest stand characteristics (Petrie et al., 2016; 2023). In undisturbed forests, ponderosa pine regeneration has been documented as large pulses of germination initiated by periods of high rainfall and warm (but not hot) summer temperatures (Schubert, 1974; Petrie et al., 2016; Rank et al., 2022). However, regeneration can also occur at low magnitudes at a consistent rate through time, leading to more favorable seedling and juvenile tree densities that support forest health and wildfire resistance (Petrie et al., 2023). The third occurrence is regeneration failure – Petrie et al. (2023) found that ∼30% of undisturbed forest sites in the SWUS experienced no natural regeneration since approximately 2000. This finding reveals the uncertainty that naturally grown ponderosa pines are facing as climate forecasts call for higher temperatures and more severe drought conditions throughout the next century (Darmenova et al., 2013; Bradford et al., 2020). Increases in the intensity of disturbances such as drought and wildfire are expected to produce smaller climatic windows of ponderosa pine regeneration in the future (Savage et al., 2013). Forest management aimed at encouraging natural regeneration of ponderosa pine has been studied previously, yet the results are highly variable across treatments, environments, and time (Wasserman et al., 2022). While the abiotic controls of regeneration in ponderosa pine are often studied (Rother et al., 2015; Hankin et al., 2019), biotic factors such as stress tolerance are less understood and could be a key factor in shaping regeneration success and failure across different environments.

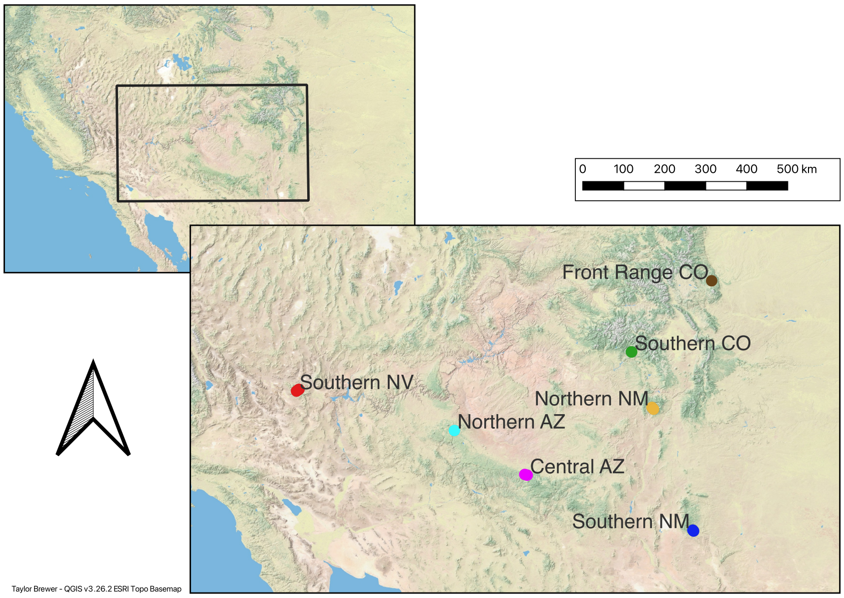
Stress tolerance may be an important and underrepresented component of ponderosa pine regeneration in the SWUS. Following germination, juvenile trees face a wide range of abiotic and biotic mortality factors (Petrie et al., 2016; Stevens-Rumann et al., 2022). Unlike established adult trees, ponderosa pine seedlings and juveniles are highly influenced by surface microclimate (Johnson et al., 2011), and their inability to acclimate above- and below-ground growth in differing environments makes them vulnerable to changes in near-surface environmental conditions (Pirtel et al., 2021). Both sustained high temperatures (Rank et al., 2022; Petrie et al., 2023) and periods of water deficit (Sapes and Sala, 2021) have been found to initiate seedling and juvenile ponderosa pine death. Kolb et al. (2020) found that in the first two years of growth, over 90% of naturally growing ponderosa pine seedlings experienced death by desiccation, and in a field experiment Koehn et al. (2022) found that relatively short periods of moisture deficit initiated mortality in planted ponderosa pines. With widespread drought-induced mortality and regeneration failures (Minott and Kolb, 2020; Petrie et al., 2023) occurring in ponderosa pine forests across the SWUS, identifying differences in stress tolerance could provide insight into how juvenile ponderosa pine vulnerability could vary across environments.

Analyzing hydraulic vulnerability could improve our ability to detect vulnerable populations of ponderosa pine. During periods of high water stress the xylem is under increased tension and can lead to cavitation of the cells and formation of embolisms, or air bubbles, that reduce water conductivity from roots to leaves (Tyree and Sperry, 1989; Brodribb and Hill, 2000). Sustained xylem tension eventually results in failure of the hydraulic system (Tyree and Sperry, 1989), which is the primary cause of conifer death during drought (Anderegg et al., 2016; McDowell et al., 2016; Adams et al., 2017). Evidence shows that intraspecies variation in ponderosa pine exists across local climates (Rehfeldt et al., 2014b; Putz et al., 2021), environments (Kerr et al., 2015; Kolb et al., 2016), and populations (Martinez-Berdeja et al., 2019; Dixit et al., 2021), yet it is unclear if these differences include hydraulic vulnerability and/or juveniles. Three different studies using the same methodology and samples from adult trees found that ponderosa pine was the most vulnerable to cavitation of the xylem within the Pinaceae family (Martinez-Vilalta et al., 2004). Hydraulic vulnerability has been associated with growing season climate (temperature and precipitation) in other conifers (He et al., 2020; Liu et al., 2021) and soil water potential in ponderosa pine (Sapes and Sala, 2021). Despite evident links between tree hydraulic functioning, climate forcings, and environmental characteristics, researchers have found considerable variation in the hydraulic vulnerability of individual ponderosa pine adults (Piñol and Sala, 2000; Stout and Sala, 2003; Koepke and Kolb, 2013; Anderegg and Hillerislambers, 2015; Clute et al., 2021). While most information on ponderosa pine vulnerability involves interspecies and adult tree comparisons, the relationship between stress tolerance and the development of hydraulic traits within this species is still unclear, particularly for juveniles (Domec et al., 2009) and trees growing in varying environments (Maherali and DeLucia, 2000; Stout and Sala, 2003; Clute et al., 2021). For seedlings and juveniles, the requirement of destructive sampling (Sperry, Donnelly, and Tyree, 1988) makes obtaining a large volume of samples challenging. Additionally, previous studies have shown high variation in hydraulic traits of seedlings (Maherali et al., 2002; Koehn et al., 2022).

An important component of regeneration-associated forest persistence may be the degree to which juveniles can withstand climate- and environmental-induced stress, and if they exhibit significant variation in vulnerability across subregional locations. Studies have shown that is not yet possible to measure the hydraulic vulnerability of ponderosa pine seedlings ($<$ 5 years; Domec and Gartner, 2003; Domec et. al., 2009), yet analyzing older juveniles may offer insight on the potential for hydraulic vulnerability to shape ponderosa pine regeneration success and failure. We present the results from 110 juvenile (~20-30 yrs. old) and 45 adult (> 50 yrs. old) ponderosa pines collected from 12 managed and unmanaged juvenile sites and 3 adult sites – a subset of 7 sub-regional study locations across the SWUS. Our objectives were to (1) determine if hydraulic vulnerability differed between adult and juvenile ponderosa pines, (2) and/or between juvenile ponderosa pines growing in climatically varying locations, (3) determine if climate and environmental conditions were associated with these differences, and (4) attribute variation in juvenile ponderosa pine vulnerability to tree growth (height and diameter). Juvenile ponderosa pines have lower water use efficiency (Grulke and Retzlaff, 2001; Knapp and Soulé, 2011; Irvine et al., 2004) and growth that is more sensitive to changes in climate (Hankin et al., 2019) compared to their adult counterparts. These physiological differences between life stages led us to hypothesize that hydraulic vulnerability would differ between juvenile and adult ponderosa pines as well. Due to previous work suggesting ponderosa pine seedlings of arid climate origin have higher plasticity of drought tolerant traits (de la Mata et al., 2022; Wu et al., 2022), we hypothesized that juvenile ponderosa pines growing in locations with greater meteorological and soil moisture deficit would have greater resistance to xylem cavitation. In adults of many tree species, height has been shown to increase hydraulic vulnerability (Couvreur et al., 2018; Choat et al., 2018), however, this relationship has not been identified in juvenile ponderosa pines. Therefore, we hypothesized that greater tree height will decrease resistance to cavitation in juvenile ponderosa pines. To date, this is the first study to investigate the hydraulic vulnerability of juvenile ponderosa pines over a large regional area.

Site Description

Our forest locations encapsulated a range of climate regimes in the SWUS, however, they provide a more limited view of environmental conditions such as species composition, topography, soil and edaphic properties, disturbances, and human management. Our study sites comprised 6 ponderosa pine forest locations in Arizona, Colorado, New Mexico, and Nevada, and successfully capture regional diversity in warm season and cool season climate conditions across the SWUS (Figure 2.1; Table 2.1). Based on daily meteorological estimates (DayMet; Thornton et al., 2022) from 1990-2020, mean annual precipitation at our study sites reached a warm season low of 163 mm (southern Nevada) and a cool season high of 365 mm (southern Colorado; Table 2.1). Locations in Arizona and New Mexico experienced a bi-modal pattern of seasonal precipitation (P: mm), with higher, monsoon-derived rainfall in summer (Sheppard et al., 2002), southern Colorado experienced seasonally consistent P and a short early summer dry period (Mahoney et al., 2015), and southern Nevada experienced very low warm season P (Pan et al., 2011). Mean air temperature ranged from -8 °C in the cool season (southern Colorado) to 23 °C in the warm season (central Arizona and southern New Mexico; 1990-2020 DayMet; Thornton et al., 2022; Table 2.1).



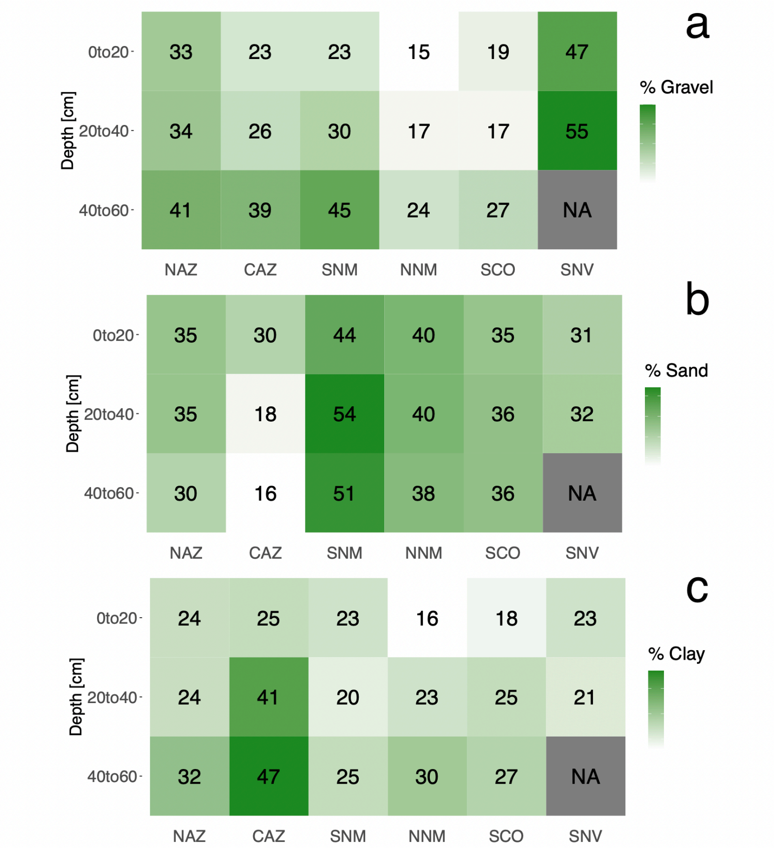
Taylor Brewer - QGIS v3.26.2 ESRI Topo Basemap

Figure 2.1: Map of southwestern US study locations.

Table 2.1: Summary of warm season (April-September) and cool season (October-March) meteorological variables from 1990-2020 for each study location, including total precipitation [P: mm], total potential evapotranspiration [E_p: mm], P-E_p, and daily minimum and maximum air temperature [T_a min, max: °C]. Values include the mean ± one standard deviation.

Location	Mean Precipitation [P: mm]	Mean E_p [mm]	Mean (P - E_p) [mm]	Mean Daily Air Temp. (max) [T_a max: °C]	Mean Daily Air Temp. (min) [T_a min: °C]
A. Warm Season (April–September)					
Northern AZ	282.3 ± 90.2	791.3 ± 13.7	-508.9 ± 92.7	22.1 ± 5.6	3.9 ± 5.2
Central AZ	306.8 ± 79.9	778.5 ± 12.1	-471.7 ± 82.1	23.3 ± 0.8	6.8 ± 1.0
Southern NM	392.1 ± 141.2	797.0 ± 12.0	-404.9 ± 144.3	22.6 ± 0.8	8.1 ± 0.9
Northern NM	293.3 ± 94.9	704.0 ± 11.8	-410.7 ± 101.9	21.9 ± 1.0	5.3 ± 0.9
Southern CO	314.7 ± 105.1	659.6 ± 13.4	-344.9 ± 113.6	21.7 ± 1.1	4.1 ± 1.3
Southern NV	163.4 ± 92.8	799.8 ± 20.7	-636.4 ± 89.4	19.6 ± 1.1	4.7 ± 2.1
B. Cool Season (October–March)					
Northern AZ	290.1 ± 117.8	248.7 ± 7.9	41.4 ± 120.7	9.3 ± 6.0	-6.8 ± 5.2
Central AZ	270.5 ± 91.1	250.9 ± 6.6	19.6 ± 94.3	10.9 ± 1.0	-4.2 ± 1.2
Southern NM	186.9 ± 80.0	337.6 ± 8.2	-150.7 ± 83.2	11.5 ± 0.8	-2.4 ± 1.0
Northern NM	241.1 ± 69.0	191.9 ± 4.9	49.1 ± 71.6	8.2 ± 1.0	-6.3 ± 0.9
Southern CO	364.9 ± 117.4	151.3 ± 5.1	213.6 ± 119.5	7.6 ± 1.1	-7.9 ± 1.5
Southern NV	362.2 ± 190.9	189.0 ± 9.5	173.2 ± 194.2	7.9 ± 1.2	-5.2 ± 2.3

Species composition of ponderosa pine forests in the SWUS can include non-competing associations with oaks (*Quercus spp.*), junipers (*Juniperus spp.*), or other pines (*Pinus spp.*; Alexander et al., 1984; Muldavin et al., 1996; Reynolds et al., 2013). Our study sites were dominated by Rocky Mountain ponderosa pine (*Pinus ponderosa var. scopulorum*), and at one mixed conifer site in southern Nevada *P. ponderosa* co-dominated with white fir (*Abies concolor*) and Rocky Mountain Douglas-fir (*Pseudotsuga menziesii var. glauca*; Pirtel et al., 2021). Physiographic features such as slope varied greatly across study sites (2-30%), but elevation ranged 2268-2503 m (Table 2.2). Soil texture and composition varies spatially across the SWUS and can have significant impacts on ponderosa pine distribution (Abella and Covington, 2006), regeneration (Puhlick et al., 2012; 2021), and growth (Knutson and Pyke, 2008). Some variation in soil texture can be seen in southern Nevada (higher gravel content), southern New Mexico (higher sand content), and central Arizona (lower sand content, higher clay content; Figure 2.2).



	NAZ	CAZ	SNM	NNM	SCO	SNV
0to20	33	23	23	15	19	47
20to40	34	26	30	17	17	55
40to60	41	39	45	24	27	NA

	NAZ	CAZ	SNM	NNM	SCO	SNV
0to20	35	30	44	40	35	31
20to40	35	18	54	40	36	32
40to60	30	16	51	38	36	NA

	NAZ	CAZ	SNM	NNM	SCO	SNV
0to20	24	25	23	16	18	23
20to40	24	41	20	23	25	21
40to60	32	47	25	30	27	NA

Figure 2.2: Heatmaps illustrating the soil texture (% gravel, % sand, % clay) from 0-20 cm (Panel a), 20-40 cm (Panel b), and 40-60 cm soil depths (Panel c) at each study location. Soil texture values were not available for SNV due to the presence of a below-ground restrictive feature.

Many authors report insect attacks (McHugh et al., 2003; Negrón et al., 2009; Fettig et al., 2010) or high severity wildfires (Owen et al., 2017; Haffey et al., 2018; Woolman et al., 2022) in SWUS ponderosa pine forests. In this study, we avoided sites disturbed by wildfire or insect attack to eliminate confounding stressors experienced by study juveniles. Common management treatments in SWUS ponderosa pine forests include density-reduction thinning and prescribed burning, which often aim to replicate historic conditions to improve forest resilience and growth (Sala et al., 2005; Stoddard et al., 2021). Forest management across our study sites included combinations of understory burning, over- and understory thinning, mowing, or no management. Two sites were treated with overstory thinning and understory burning (northern and central Arizona), five sites were treated with over- and understory thinning (central Arizona and New Mexico, southern New Mexico, Colorado, and Nevada), and one site was treated with overstory thinning, understory burning, and mowing (southern Colorado; Table 2.2). We considered one managed site in central Arizona and southern Colorado representative of unmanaged due to a lack of consistent treatment.

Table 2.2: Characteristics of sampling sites at each study location, including management classification [T = Overstory thinning; U = Understory thinning; M = Mowing, B = Understory burning, and N = Unmanaged.], elevation [m], slope [%], mean diameter at breast height of adult trees [DBH: cm], cone density [No. m^{-2}], basal area [m^{2} ha^{-1}], canopy cover [%], and understory cover [shrub, herbaceous, and litter cover: %].

Sample Site	Management Class	Elevation [m]	Slope [%]	Mean DBH [cm]	Cone Density [No. m^{-2}]	Basal Area [m^{2} ha^{-1}]	Canopy Cover [%]	Shrub Cover [%]	Herb. Cover [%]	Litter Cover [%]
Northern AZ	TB	2245	7	42.9	2.6	28	57.2	0.0	34.6	85.9
Central AZ	TB	2219	2	27.0	1.8	18	46.8	5.0	19.5	90.6
	TU	2341	2	31.5	1.5	16	37.4	11.8	17.5	85.0
Southern NM	N	2345	21	14.7	1.6	22	69.9	1.2	30.6	92.8
	TU	2310	6	34.7	1.4	14	23.1	28.3	16.4	82.4
Northern NM	N	2468	7	25.7	0.3	34	49.9	0.0	10.2	90.0
	TU	2461	8	30.8	1.3	24	39.7	0.0	15.0	88.1
Southern CO	TU	2445	3	32.0	0.3	26	60.1	29.4	46.9	81.3
	TBM	2458	6	27.9	1.0	16	42.9	5.6	14.7	75.0
Southern NV	N	2601	30	11.6	3.1	20	50.5	13.6	8.0	82.4
	N	2482	8	7.0	5.5	10	42.6	1.9	2.4	92.8
	TU	2497	14	32.8	1.1	16	36.1	0.0	4.0	88.8

Methods

2021 field sampling and site characterization

In summer 2021, we collected 176 juvenile ponderosa pine stems in the field from 12 ponderosa pine forest sites in 6 SWUS locations: northern Arizona (1 site; 24 stem samples), central Arizona (2 sites; 24 stem samples), southern New Mexico (2 sites; 24 stem samples), northern New Mexico (2 sites; 28 stem samples), southern Colorado (2 sites; 28 stem samples), and southern Nevada (3 sites; 44 stem samples; Figure 2.1; Table 2.3). The average ground-line diameter (GLD: mm) of sampled juvenile trees was 45 ± 16 mm, and their average height (mm) was 1314 ± 480 mm (Table 2.3). We estimate that most trees sampled were approximately 20-30 years old. To compare juvenile trees to adults, we collected an additional 46 adult (> 50 years old) ponderosa pine stems from 3 forest sites at the Manitou Experimental Forest in Colorado (Figure 2.1; Table 2.3).

Table 2.3: Study locations [latitude: °N; longitude: °W], attributes of sampled juvenile ponderosa pines [ground-line diameter, GLD: mm; height: mm; p50: MPa; $\bar{x} \pm$ one standard deviation], and summary of tree branch samples analyzed for managed and unmanaged sites at each study location. Juvenile ponderosa pine stems were collected from 6 locations in the southwestern US (Part A), and adult ponderosa pine stems were collected at a Front Range Colorado location (Part B). Field samples refers to the total number of stems analyzed, whereas usable samples is the number of analyzed stems that provided usable data. Letters indicate statistically different means, determined by ANOVA and Tukey's honest significant difference tests ($p < 0.05$). Study locations are abbreviated as: NAZ = northern Arizona; CAZ = central Arizona; SNM = southern New Mexico; NNM = northern New Mexico; SCO = southern Colorado; and SNV = southern Nevada.

A. Juvenile tree locations

Study Location	Latitude [°N]	Longitude [°W]	Mean GLD [mm]	Mean Height [mm]	Mean p50 [MPa]	Field Samples	Usable Samples	Managed Trees	Unmanaged Trees
Northern AZ	35.27318	−111.68430	38 ± 6^{b}	899 ± 230^{c}	-4.54 ± 0.75^{ab}	24	17	17	–
Central AZ	34.13772	−109.85186	36 ± 8^{b}	1105 ± 269^{bc}	-4.06 ± 0.96^{a}	24	15	5	10
Southern NM	32.70759	−105.57120	41 ± 9^{b}	1328 ± 289^{ab}	-3.72 ± 0.86^{a}	24	17	8	9
Northern NM	35.84280	−106.60759	44 ± 11^{b}	1602 ± 568^{a}	-4.63 ± 0.62^{ab}	24	14	7	7
Southern CO	37.28798	−107.15065	47 ± 11^{b}	1296 ± 372^{ab}	-4.26 ± 0.79^{a}	28	23	11	12
Southern NV	36.31007	−115.68938	59 ± 24^{a}	1588 ± 601^{a}	-5.05 ± 1.16^{b}	44	24	5	19
$\bar{x} \pm$ SD			45 ± 16	1314 ± 480	-4.41 ± 0.98				
Total						222	110	53	57
B. Adult tree location									
Front Range CO	39.11100	−105.10000	–	–	-3.90 ± 1.16	46	45	15	13

We characterized sampling sites in summer 2021 using a circular plot sampling method described in Pirtel et al. (2021). Site characterization measurements included elevation (m), slope (%), mean diameter at breast height of adult trees (DBH: cm), cone density (No. m^{-2}), basal area (m^2 ha^{-1}), canopy cover (%), understory cover (% litter, % herbaceous, and % shrub cover; Table 2.2), and surface (0-10 cm depth) soil characteristics (pH; sand, silt, clay, and organic matter: %). Unmanaged sites were without human management for ∼20+ years, whereas managed sites experienced a variety of human interventions including overstory thinning (T), understory thinning (U), understory burning (B), and mowing (M; Table 2.2). Data from field research are published online (Petrie et al., 2023).

Laboratory analysis and p50 measurements

We collected juvenile and adult ponderosa pine stems (> 5.0 mm in diameter and > 20.0 cm in length) in the field using a pruning tool. Stems were cut to approximately 20.0 cm length while submerged in distilled water, wrapped in a damp paper towel, and sealed in a plastic bag. Following sampling at each site, we shipped samples 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 an appropriate temperature to prevent damage to the stems.

Once in the lab, stems were cut again to approximately 14.0 cm length while submerged in distilled water, and we removed 1.5 cm of bark on both ends. We then sealed the barked portion of the stem segment with adhesive and polytetrafluoroethylene (PTFE) film tape, and then in a wet paper towel to prevent drying during the analysis. For the analysis, we fit stem segments into a tubing manifold and vacuum flushed segments with degassed, filtered water to remove prior embolisms or resin, and to refill stem conduits. This ensured the same initial state for all stem samples prior to taking conductance measurements. We equilibrated the system and then measured the background flow rate of the stem segment, which is flow lacking a pressure influence. We then measured the pressurized flow by inducing a hydraulic head on the stem segment using an elevated IV bag. We repeated the background measurements and then removed the stem from the apparatus. We used the cavitron method to measure hydraulic vulnerability, which induces continuous negative pressures (MPa) on the stem segments and a positive hydrostatic pressure difference across the sample (Cochard, 2002). We preferred this method 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. We measured hydraulic conductance of each stem segment using a specialized rotor attached to a centrifuge (Du Pont Sorvall RC–5B). We fit stem segments into the rotor and placed the exposed ends in reservoirs of filtered water. We then spun the centrifuge at increasing angular velocities to induce more negative pressures (0.5 MPa increments) until complete cavitation of the sample was reached.

In total, we collected 222 stems in the field (46 adult; 176 juvenile), and of these 155 stems (70%) provided usable data (45 adult, 98%; 110 juveniles, 63%; Table 2.3). Sample errors were caused by irreparable embolization of stem conduits, excessive resin blocking flow through the xylem, and conductance irregularities that prevented accurate measurement.

We used R program *conductoR* (Bacher, 2022) to record and calculate conductance measurements from an electronic balance. We then used the R program $fitplc$ to generate percent loss values, predict p50 with confidence intervals using non-parametric bootstrap, and fit vulnerability curves (Duursma and Choat, 2017). P50 is the point at which 50% of the xylem conductance is lost due to cavitation of the stem conduits and is commonly reported in plant hydraulic studies (Machado and Tyree, 1994; Brodribb et al., 2010; Xie et al., 2022). More negative p50 values indicate greater levels of embolism resistance (Hacke et al., 2001b).

Meteorological estimates and SOILWAT2 water balance simulations

To explore how environmental demand and soil-water dynamics influence juvenile ponderosa pine hydraulic vulnerability at our study sites, we used the SOILWAT2 model to simulate these variables. SOILWAT2 is a daily time step, process-based, one dimensional, deterministic model that simulates water balance dynamics across multiple soil layers (Schlaepfer and Andrews, 2019; Schlaepfer and Murphy, 2019). The model incorporates observational and spatial data of meteorological conditions, landscape features, and ecosystem attributes to deliver an array of temperature and soil-water estimates that provide insight on the climate-driven conditions anticipated to influence hydraulic vulnerability. SOILWAT2 has effectively simulated ecohydrological and temperature dynamics across ponderosa pine forests of many different climates and forest stand characteristics (Bradford and Bell, 2017; Petrie et al., 2017; 2020).

We parameterized each study site in SOILWAT2 integrating (1) topographic features such as elevation, slope, and aspect, (2) forest stand characteristics including canopy cover, basal area, understory vegetation (herbaceous, shrub) and cover (litter, coarse woody debris), and (3) near-surface (0-10 cm) and sub-surface (> 10 cm) soil properties. For soil properties below 10 cm depth, we used POLARIS soil estimates (Chaney et al., 2019). We forced the SOILWAT2 model using Oak Ridge National Laboratory DayMet estimates from 1990-2020 at 1 km^2 resolution [https://daymet.ornl.gov/], (Thornton et al., 2022).

Meteorological estimates in our analyses included P and air temperature (T_a: °C). We used SOIL-

WAT2 to simulate potential evapotranspiration (E_p: mm; Table 2.1), soil water potential (ψ_p: MPa), and soil water content (θ: m^3 m^{-3}) at field capacity (θ_{fc}: -0.33 MPa) and wilting point (θ_{wp}: -1.33 MPa) at each study site, incorporating meteorological estimates and site characteristics. The SOILWAT2 model utilizes the Penman-Monteith equation to estimate E_p, which incorporates T_a, humidity, radiation, and wind speed (Penman, 1963). We calculated the difference between P and E_p, for each month to assess the meteorological water balance (P-E_p: mm) and evaluated all meteorological and simulated variables over two seasonal time periods: warm season (April-September) and cool season (October-March).

We utilized estimates of warm and cool season soil ψ_p ranging 0 to 50 cm depth (0-5 cm, 5-10 cm, 10-20 cm, 20-30 cm, 30-40 cm, and 40-50 cm) at each site and averaged these by location. Model estimates indicated that all locations except for southern Nevada had soil profile depths $\geq$ 100 cm. Soil estimates in southern Nevada concluded at approximately 20-30 cm and 30-40 cm due to a below-ground restrictive layer. We found that across locations, warm season soil ψ_p at depths of 5-10 cm, 10-20 cm, 20-30 cm, and 30-40 cm was not significantly different, and we combined soil layers using a weighted average (5-40 cm) to account for varying increment depths. We multiplied values by increment depth, totaled these, and divided by the desired total profile depth. We averaged cool season ψ_p depths of 0-5 cm, 5-10 cm, 10-20 cm, and 20-30 cm due to non-significant differences between layers as well (0-10 cm; 10-30 cm).

We derived sub-surface (> 10 cm) soil properties (% gravel, % sand, and % clay) from probabilistic soil properties database POLARIS (Chaney et al., 2019). Soil estimates were given in 10 cm increments ranging 0 to 60 cm depth. We then used soil textural estimates to simulate values of θ_{fc} and θ_{wp} at each site using the $rSOILWAT2$ R package (Schlaepfer and Murphy, 2023). We averaged both variables to 20 cm depth increments (0-20 cm, 20-40 cm, and 40-60 cm) and averaged sites by location.

Statistical analysis

We determined significant differences in p50 values, seasonal climate, and soil-water variables using analysis of variance (ANOVA) and Tukey's honest significant difference (HSD) tests ($p < 0.05$). We performed linear regression analyses to find significant associations between juvenile p50, soil and edaphic properties, and tree growth (height, diameter). We used R (R Core Team, 2021) for all statistical analyses and created figures using the *ggplot2* package (Wickham, 2016).

Results

Juvenile hydraulic vulnerability

Juvenile ponderosa pines from managed sites, unmanaged sites, and all sites combined had more negative p50 values than adult ponderosa pines (managed juveniles -4.40 ± 0.82 MPa; unmanaged juveniles -4.43 ± 1.12 MPa; all juveniles -4.41 ± 0.98 MPa; adults -3.90 ± 1.16 MPa; $p < 0.05$; Figure 2.3).

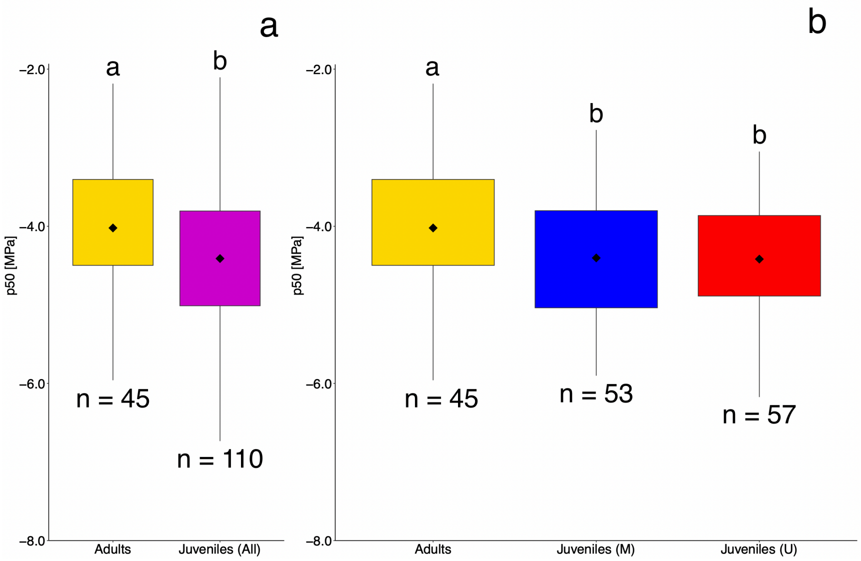


Figure 2.3: Boxplots illustrating p50 values [MPa] between all adult and all juvenile ponderosa pines (Panel a), and between adult ponderosa pines, juvenile ponderosa pines located in managed forest sites (M), and juvenile ponderosa pines located in unmanaged forest sites (U; Panel b). Letters indicate statistically different means (illustrated by the symbol in each box), determined by ANOVA and Tukey's honest significant difference tests ($p < 0.05$). The number of stem samples is provided below each box.

Juvenile ponderosa pines in southern Nevada had more negative p50 values (-5.05 ± 1.16 MPa) than juveniles in southern Colorado (-4.26 ± 0.79 MPa), southern New Mexico (-3.72 ± 0.86 MPa), and central Arizona (-4.06 ± 0.96 MPa; $p < 0.001$; Figure 2.4a). We found no significant differences in p50 of managed versus unmanaged juvenile ponderosa pines (Figure 2.4b), nor between managed versus unmanaged forest sites any SWUS location (Figure 2.4b).

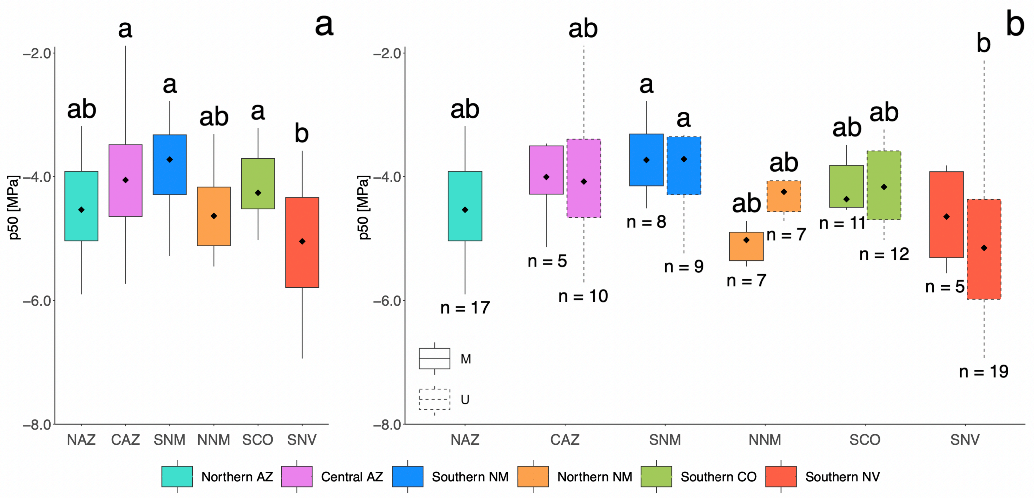


Figure 2.4: Boxplots illustrating p50 values [MPa] between juvenile ponderosa pines in different locations (Panel a), and an expanded illustration further illustrating juvenile p50 values between managed (M) and unmanaged (U) forest sites in each location (Panel b). Northern Arizona (NAZ) samples were only collected from a single managed site. Letters indicate statistically different means (illustrated by the symbol in each box), determined by ANOVA and Tukey's honest significant difference tests ($p < 0.05$). The number of stem samples is provided below each box.

Warm and cool season climate

Warm season P-E_p was significantly more severe (denoted by more negative values) in southern Nevada compared to all other SWUS locations ($p < 0.001$; Figure 2.5a,b). In southern Nevada, warm season E_p was like other SWUS locations (northern Arizona, southern New Mexico; Figure 2.5c,d), but warm season P was significantly lower than all other locations (Figure 2.5e,f).

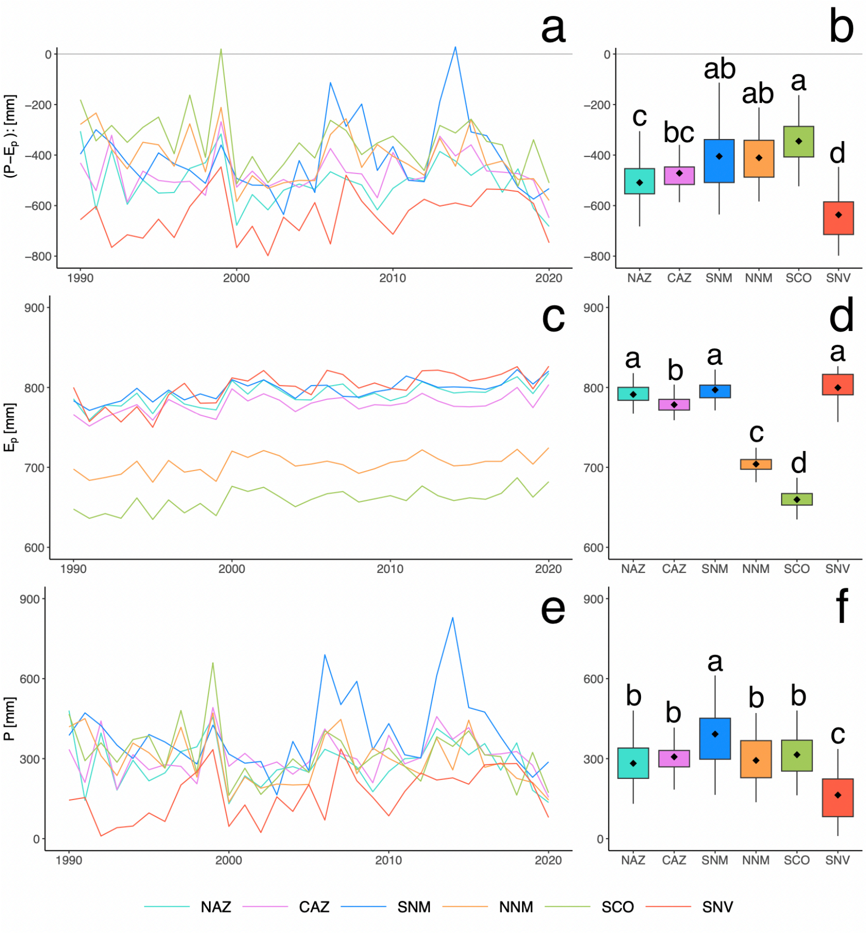


Figure 2.5: Timeseries (Panel a) and boxplots (Panel b) illustrating mean warm season (April–September) precipitation minus potential evapotranspiration [P-E$_p$: mm] from 1990–2020 for each study location, timeseries and boxplots of E$_p$ (Panels c,d), and timeseries and boxplots of P (Panels e,f). Letters in Panels b,d and f indicate statistically different means (illustrated by the symbol in each box), determined by ANOVA and Tukey's honest significant difference tests ($p < 0.05$).

Cool season P-E$_p$ was significantly more severe in southern New Mexico compared to all other SWUS locations and was significantly less severe in southern Colorado and southern Nevada ($p < 0.001$; Figure 2.6a,b). Severe cool season moisture deficit of southern New Mexico was produced by high E$_p$ (Figure 2.6c,d) and low P (Figure 2.6e,f), whereas the less severe moisture deficits of southern Colorado and southern Nevada were produced by low E$_p$ and average P relative to other SWUS sites.

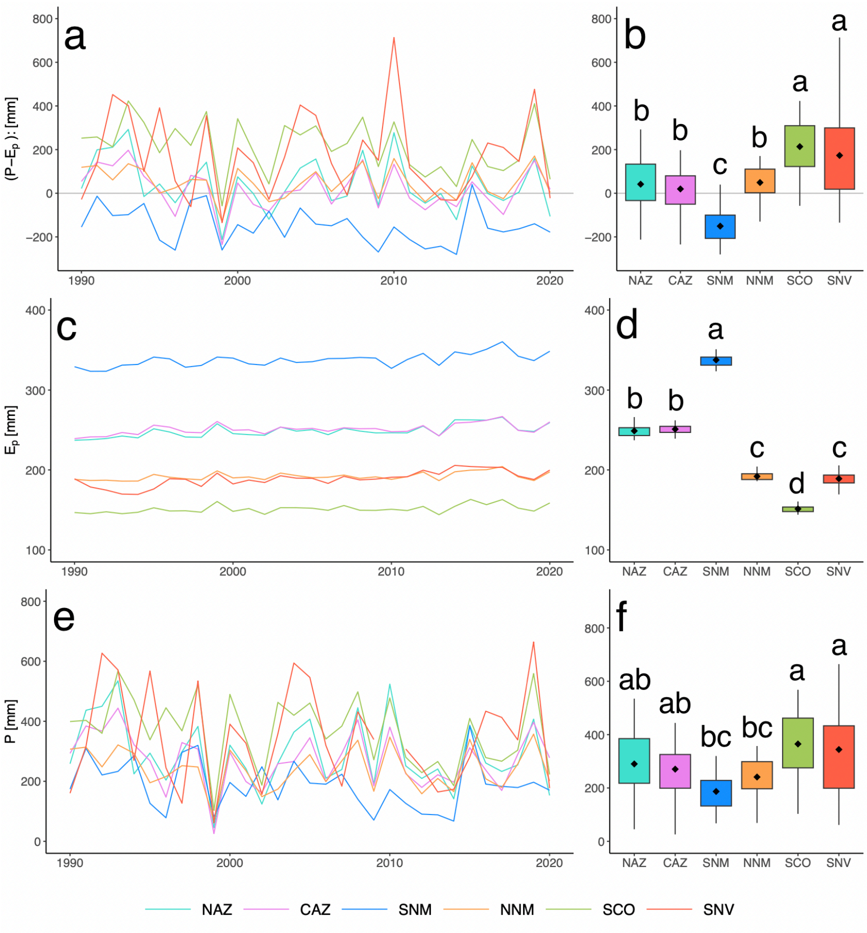


Figure 2.6: Timeseries (Panel a) and boxplots (Panel b) illustrating mean cool season (October-March) precipitation minus potential evapotranspiration [P-E_p: mm] from 1990-2020 for each study location, timeseries and boxplots of E_p (Panels c,d), and timeseries and boxplots of P (Panels e,f). Letters in Panels b,d and f indicate statistically different means (illustrated by the symbol in each box), determined by ANOVA and Tukey's honest significant difference tests ($p < 0.05$).

Warm and cool season soil water potential and soil water holding capacity

Both cool and warm season mean soil ψ_p was significantly more negative from 0-40 cm depths in southern Nevada compared to all other SWUS locations ($p < 0.001$; Figure 2.7; Figure 2.8). In the warm season, mean soil psi_p at 0-5 cm depth in southern Nevada exceeded the mean and lower limit of p50 values observed for juvenile ponderosa pines (Figure 2.5a). Soil estimates suggest a restrictive feature at approximately 40 cm depth in southern Nevada (denoted by NA; Figure 2.7c; Figure 2.8d), preventing accurate measurements.

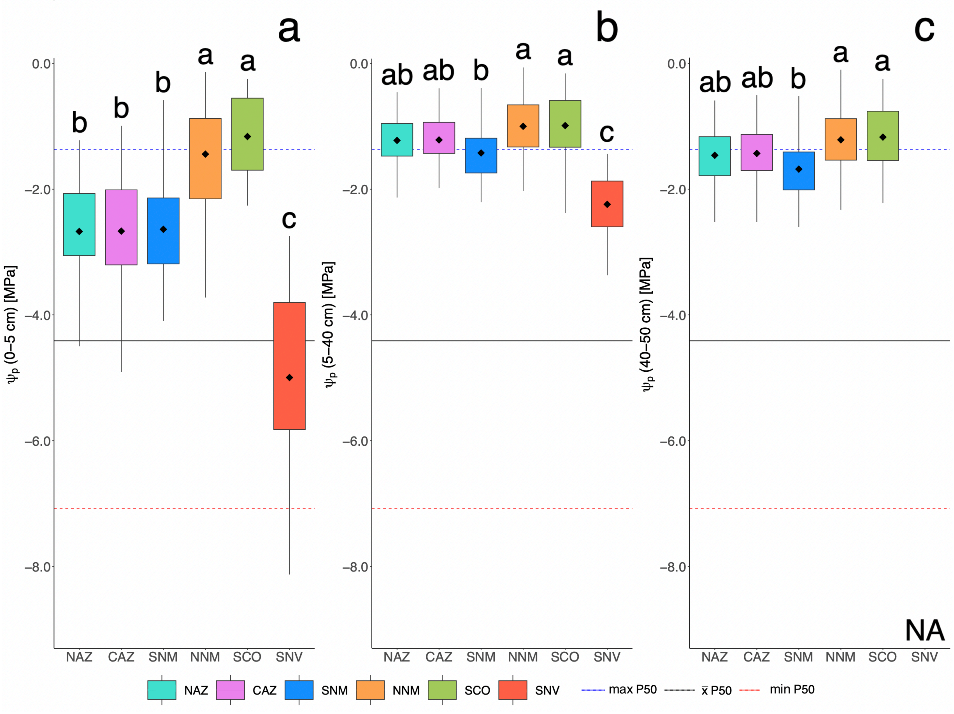


Figure 2.7: Boxplots illustrating SOILWAT2 simulations of warm season (April-September) soil water potential [ψ_p: MPa] from 1990-2020 at each study location, averaged across 0-5 cm soil depths (Panel a), 5-40 cm soil depths (Panel b), and 40-50 cm soil depths (Panel c). In each panel, the horizontal black line indicates the mean p50 value of juvenile ponderosa pines, the red line indicates the most negative p50 value we observed, and the blue line indicates the least negative p50 value we observed. Letters indicate statistically different means (illustrated by the symbol in each box), determined by ANOVA and Tukey's HSD tests ($p < 0.05$). Soil water potential simulations were not conducted at 40-50 cm depth in SNV due to the presence of a below-ground restrictive feature.

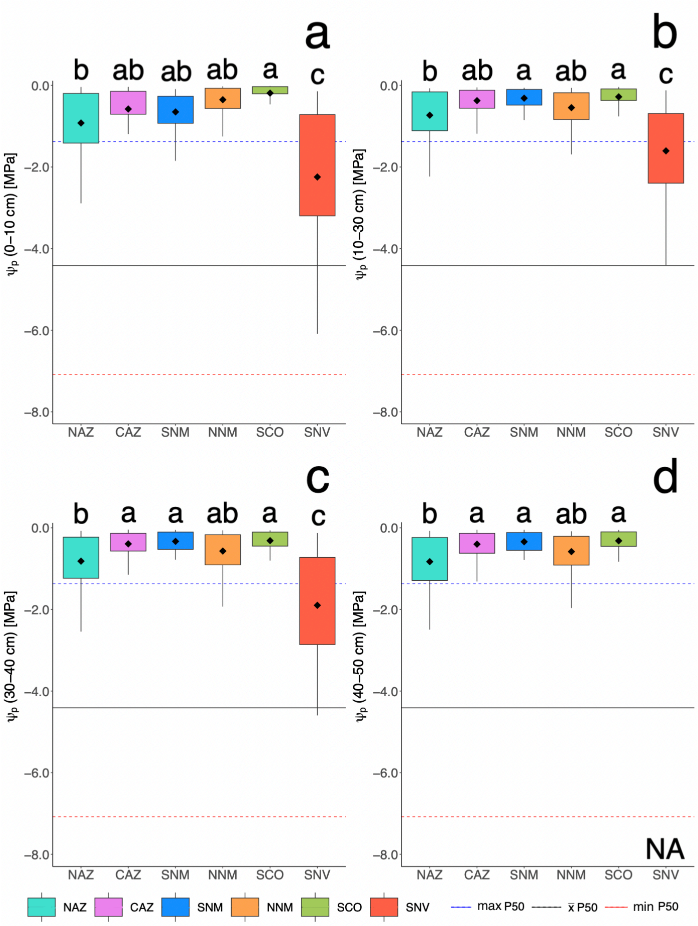


Figure 2.8: Boxplots illustrating SOILWAT2 simulations of cool season (October-March) soil water potential [ψ_p: MPa] from 1990-2020 at each study location, averaged across 0-10 cm soil depths (Panel a), 10-30 cm soil depths (Panel b), 30-40 cm soil depths (Panel c), and 40-50 cm soil depths (Panel d). In each panel, the horizontal black line indicates the mean p50 value of juvenile ponderosa pines in our analysis, the red line indicates the most negative p50 value we observed, and the blue line indicates the least negative p50 value we observed. Letters indicate statistically different means (illustrated by the symbol in each box), determined by ANOVA and Tukey's HSD tests ($p < 0.05$). Soil water potential simulations were not conducted at 40-50 cm depth in SNV due to the presence of a below-ground restrictive feature.

Soils in southern Nevada had higher estimated gravel content (mean SNV gravel: 52%; mean SWUS gravel: 28%; Figure 2.2) and lower soil water holding capacity from 0–40 cm depth compared to all other SWUS locations (mean SNV θ_{fc}: 0.16 m^3 m^{-3}, θ_{wp}: 0.09 m^3 m^{-3}; mean SWUS θ_{fc}: 0.22 m^3 m^{-3}, θ_{wp}: 0.13 m^3 m^{-3}; Figure 2.9).

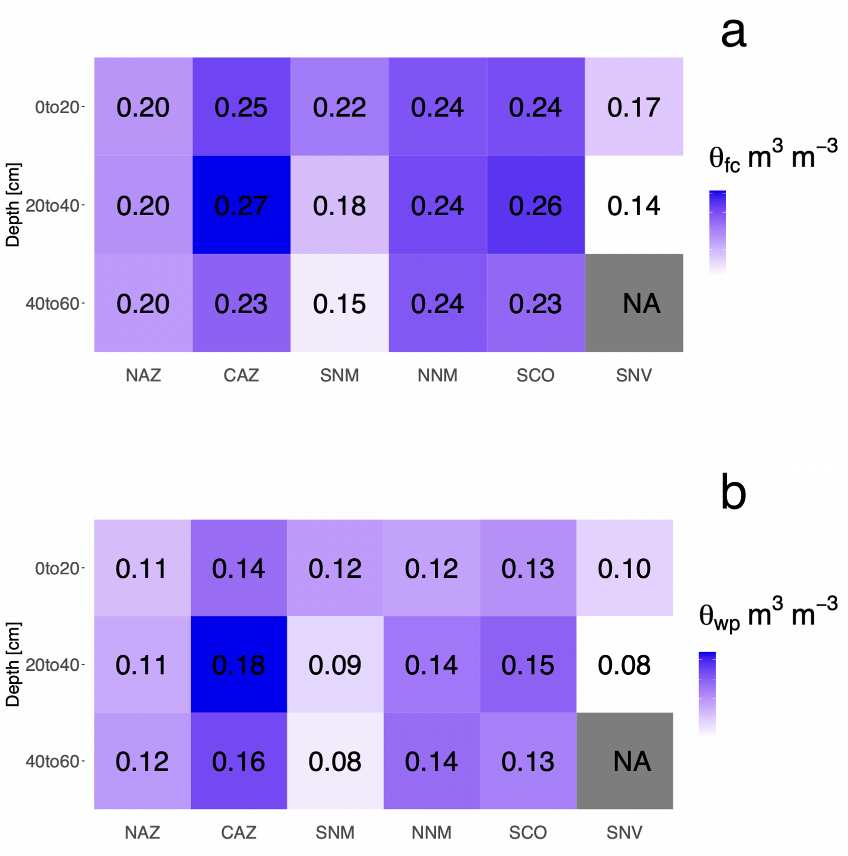


Figure 2.9: Heatmaps illustrating estimated volumetric soil moisture [θ: m^3 m^{-3}] at soil field capacity [θ_{fc}: -0.033 MPa] at 0-20 cm, 20-40 cm, and 40-60 cm soil depths (Panel a), and estimated volumetric soil moisture at soil wilting point [θ_{wp}: -1.5 MPa] at 0-20 cm, 20-40 cm, and 40-60 cm soil depths (Panel b). Estimations were not conducted below 40 cm depth in SNV due to the presence of a below-ground restrictive feature.

Edaphic and tree growth factors broadly associated with juvenile p50

Significant negative linear correlations occurred between soil clay content (0-10 cm depth), soil pH (0-10 cm depth), and average p50 of juvenile ponderosa pines at our study sites ($p < 0.05$; Figure 2.10). We note that these relationships were non-significant when southern Nevada sites were removed (Figure 2.10b,d) – where sites had higher average soil pH values and one site had a more negative average p50 value. Average p50 of juvenile ponderosa pines was more highly correlated to soil pH than soil clay content ($R^2 = 0.51$ and 0.33, respectively; Figure 2.10).

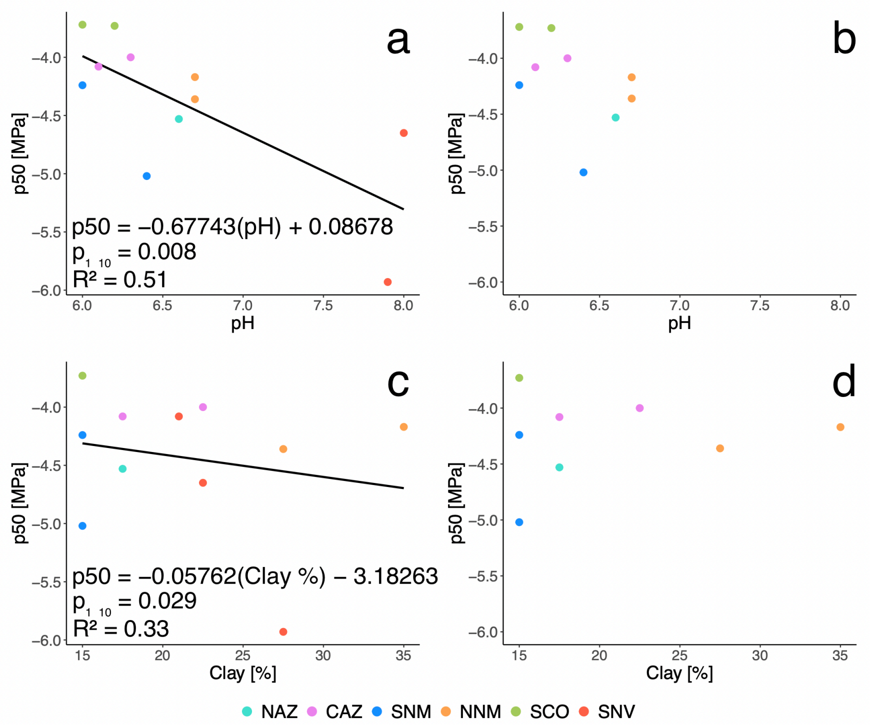


Figure 2.10: Linear relationships between soil pH (0-10 cm depth) and mean p50 [MPa] (Panel a), pH and mean p50 with SNV trees omitted (Panel b), soil clay content (%; 0-10 cm depth) and mean p50 (Panel c), and soil clay content and mean p50 with SNV trees omitted (Panel d) for juvenile ponderosa pines. Significant relationships were determined using linear correlations (R^2 coefficient of determination, $p < 0.05$).

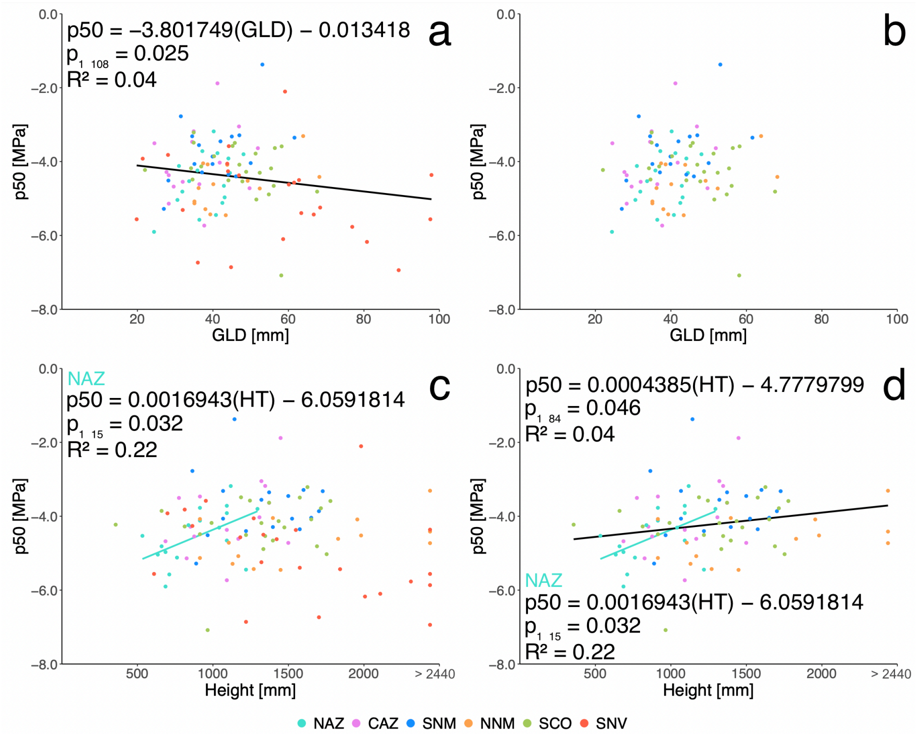


Figure 2.11: Linear relationships between ground-line diameter [GLD: mm] and mean p50 [MPa] (Panel a), GLD and mean p50 with SNV trees omitted (Panel b), tree height [mm] and mean p50 (Panel c), and height and mean p50 with SNV trees omitted (Panel d) for juvenile ponderosa pines. Significance was determined using linear correlations (R^2 coefficient of determination, $p < 0.05$). When significant, linear correlations are shown for all juveniles, as well as for individual study locations. A small number of trees were taller than we could measure from the ground, and are indicated by "> 2440" (Panels c and d).

Significant negative linear correlations were found between GLD, height, and average p50 of juvenile ponderosa pines ($p < 0.05$; Figure 2.11). We note that the relationship between GLD and p50 was non-significant when southern Nevada juveniles were omitted (Figure 2.11b) – where juveniles had greater GLD values. On the contrary, the correlation between juvenile height and p50 was revealed upon omitting southern Nevada juveniles (Figure 2.11d). Juveniles in southern Nevada were much taller than those of other sites and exerted considerable influence over the correlation. Both GLD and height were weakly correlated to juvenile p50 across sites ($R^2 = 0.04$; Figure 2.11). A significant positive linear relationship occurred between height and p50 for juveniles in northern

Arizona ($p < 0.05$, $R^2 = 0.22$; Figure 2.11c,d) – the only location of our study to exhibit a significant relationship individually.

Table 2.4: Summary of ANOVA analyses performed in this study and respective statistics [p = p value, df = degrees of freedom, F = F value, SS = sum of squares, MS = mean of squares, and Adj. R^2 = adjusted coefficient of determination]. Depth [cm] indicates soil depth. Warm season (April-September; Section A) and cool season (October-March; Section B) variables include precipitation [P: mm], potential evapotranspiration [E_p: mm], meteorological moisture balance [P-E_p: mm], and soil water potential [ψ_p: MPa]. In Section C, M/U represents managed (M) and unmanaged (U) juvenile ponderosa pines.

A. Cool season (October-March) ANOVA table

$y \sim$ *Location*	Depth [cm]	p	df	F	SS	MS	Adj. R^2
P-E_p [mm]	–	$< 2.2e^{-16}$	5, 180	35.236	256917	513833	0.4806
E_p [mm]	–	$< 2.2e^{-16}$	5, 180	2577.5	671838	671838	0.9858
P [mm]	–	$4.724e^{-9}$	5, 180	10.744	748295	149659	0.2085
ψ_p [MPa]	0–10	$< 2.2e^{-16}$	5, 240	24.629	112.55	22.511	0.3253
	10–30	$< 2.2e^{-16}$	5, 240	30.476	51.432	10.286	0.3756
	30–40	$< 2.2e^{-16}$	5, 240	36.945	75.554	15.111	0.4232
	40–50	$3.64e^{-7}$	4, 200	9.6646	7.499	1.875	0.1452

B. Warm season (April-September) ANOVA table

$y \sim$ *Location*	Depth [cm]	p	df	F	SS	MS	Adj. R^2
P-E_p [mm]	–	$< 2.2e^{-16}$	5, 180	28.844	1621437	324287	0.4294
E_p [mm]	–	$< 2.2e^{-16}$	5, 180	525.44	537258	107452	0.9341
P [mm]	–	$3.869e^{-13}$	5, 180	16.144	849227	169845	0.2904
ψ_p [MPa]	0–5	$< 2.2e^{-16}$	5, 240	74.434	375.37	75.07	0.5998
	5–40	$< 2.2e^{-16}$	5, 240	41.569	44.470	8.894	0.4529
	40–50	$6.09e^{-5}$	4, 200	6.5062	6.941	1.7353	0.0974

C. p50 ANOVA table

$y \sim$ *Adults vs. Juveniles*		p	df	F	SS	MS	Adj. R^2
p50 [MPa]	–	0.02037	1, 153	5.4938	4.861	4.8606	0.0284
$y \sim$ *Adults vs. Juveniles (M/U)*							
p50 [MPa]	–	0.02399	2, 152	3.8233	6.717	3.3583	0.0354
$y \sim$ *Location*							
p50 [MPa]	–	$2.896e^{-5}$	6, 148	5.6030	25.958	4.3260	0.1521
$y \sim$ *Site*							
p50 [MPa]	–	0.002157	10, 99	3.0360	24.472	2.4472	0.1574

D. Tree attributes ANOVA table

$y \sim$ *Location*		p	df	F	SS	MS	Adj. R^2
Height [mm]	–	$7.396e^{-6}$	5, 103	7.2559	6470831	1294166	0.2246
GLD [mm]	–	$1.069e^{-5}$	5, 104	7.0312	6653.50	1330.70	0.2167

Discussion

We measured the hydraulic vulnerability of juvenile (∼20-30 years old) ponderosa pines growing in 6 climatically-varying locations of the SWUS and evaluated how seasonal climate, environmental conditions, and tree growth were associated with differences in vulnerability. Due to previous work suggesting ponderosa pine seedlings originating from hot/dry climates have higher plasticity of drought tolerant traits (de la Mata et al., 2022; Wu et al., 2022), we hypothesized that juvenile ponderosa pines growing in locations with greater meteorological and soil moisture deficit would have greater resistance to xylem cavitation. We found support for this only at the driest location, where juveniles growing in southern Nevada displayed more negative p50 values than juveniles in southern Colorado, southern New Mexico, and central Arizona. Compared to all other SWUS locations, southern Nevada had significantly more severe warm season meteorological moisture deficit, lower warm and cool season soil ψ_p, and lower soil water holding capacity. Despite relatively high cool season precipitation at this location, shallow soil layers and high soil gravel content decreased water storage and resulted in much lower (more negative) soil ψ_p in both seasons. The association between low soil ψ_p and juvenile hydraulic vulnerability in southern Nevada is corroborated by Sapes and Sala (2021), who found that lower soil ψ_p resulted in greater hydraulic efficiency of droughted ponderosa pine seedlings. While few studies investigate intraspecies plasticity to cavitation across environments, lower p50 values associated with dry conditions have also been reported in other species and ecosystems (Corcuera et al., 2011; López et al., 2016; Stojnić et al., 2017). These findings suggest that interactions between climate and hydraulic soil properties are linked to low soil ψ_p and p50 differences found in southern Nevada.

We found that juvenile and adult (> 50 years old) ponderosa pines had significant differences in p50, suggesting that hydraulic vulnerability varies between stages of tree development. It can be reasonably assumed that adult ponderosa pines do not differ in hydraulic vulnerability, regardless of their location or environment (Maherali and DeLucia, 2000; Stout and Sala, 2003; Domec et al., 2003). We also found that vulnerability to embolism increases with height in juveniles, an association previously limited to adult trees (Courveur et al., 2018; Olson et al., 2018). Perhaps juvenile ponderosa pines begin life with plasticity in hydraulic vulnerability and their tolerance to water stress decreases with age, likely as individuals become established within their environments. It is possible that greater resistance to xylem cavitation could act as a temporary buffer to developing juveniles in other SWUS locations until their roots are able to access more consistent deep soil moisture. We also found significant associations between juvenile p50, soil pH, and soil clay content, which have also been identified as important variables to ponderosa pine regeneration (Puhlick et al., 2012). While it is likely that hydraulic vulnerability is influenced by physical and chemical soil properties, such as soil clay content and soil pH, these relationships are not conclusive and require further investigation.

Climate and soil interactions: water limitation and regeneration

Like many other dryland ecosystems, soil and edaphic properties translate climate conditions into soil moisture availability (Liu et al., 2019; Pascolini-Campbell et al., 2019) in southern Nevada. Soils across these sites are characterized by high to extremely high gravel content, thin soil layers with fractured bedrock found at relatively shallow depths, and drainage ranging from well-drained to somewhat excessively drained (Figure 2.2; Web Soil Survey, USDA). Shallow soil profile depths at this location amplified water-limited conditions in the warm season by greatly reducing the physical space in which water could be stored, and high gravel content further restricted water holding capacity of these soils. Despite sites receiving relatively high cool season precipitation and low E_p, these physical limitations yielded much lower soil ψ_p than any other study location throughout both seasons. We postulate that low soil ψ_p was a significant source of stress during early development of juvenile ponderosa pines in southern Nevada and likely resulted in more negative p50 values. Seedlings and juveniles at this location likely operate under high levels of water stress until they can access more consistent deep soil moisture. The ability for ponderosa pine to root within deeper soil layers is critical to their survival (Petrie et al., 2017), and bedrock moisture can support plant transpiration long after upper soil layers have dried (Szutu and Papuga, 2019). Sufficient water uptake from deep soil layers has been shown to decouple embolism resistance from habitat aridity (Pivovaroff et al., 2016; Choat et al., 2018), which could explain why juveniles in more favorable growing conditions did not display differences in p50. Witty et al. (2003) found that ponderosa pine seedlings growing in California's Sierra Nevada had roots reaching fractured bedrock around depths of 100 cm within their first 2 years. If this is true for juvenile ponderosa pines in southern Nevada (where fractured bedrock is present at much shallower depths; ∼40 cm) more negative p50 values could indicate excessively drying and/or very little recharge occurring at this location. The relationship between climate conditions, soil-water dynamics, and p50 in ponderosa pine might behave similar to other dryland species (Koepke and Kolb, 2013), and these interactions could shape patterns of forest persistence across the SWUS.

It is widely accepted that periods of favorable climate conditions (temperature and precipitation) are required for ponderosa pine germination and establishment, however, soil and edaphic properties are increasingly being tied to the probability and success of regeneration events (Puhlick et al., 2012; Minott and Kolb, 2020; Puhlick et al., 2021; Petrie et al., 2023). Soil properties could dictate what climate conditions are able to support regeneration, particularly at sites with unique or poor quality soils. Successful regeneration in southern Nevada might require longer periods of favorable climate conditions in the growing season that could buffer the effect of a shallow, rocky soil. Soil moisture at shallow depths is closely controlled by precipitation with even small events causing increases, but deep soil moisture increases only after large precipitation events (Szutu and Papuga, 2019). Through late spring and summer, high evapotranspiration can deplete upper layer soil moisture, and established trees often rely on deep soil layers to provide moisture until rewetting occurs (Arkley, 1981; Anderson et al., 1995). While snowmelt typically restores hydrologic connectivity between soil layers in the early spring, this moisture is quickly lost near the surface (McNamara et al., 2005) – leaving seedlings and juveniles with shallow root systems vulnerable to water stress or even mortality. In southern Sierra Nevada pine forests, Hubbert et al. (2001) found that by mid-June, winter snowmelt recharge was depleted in upper layers, and by July plant available water was found exclusively within the fractured bedrock layer. This rapid water loss and movement leaves a small window in which newly regenerated seedlings have a chance to acquire water. At locations where soil is considered more favorable, the influence of climate and stand characteristics may exert stronger control on regeneration rather than soil properties, highlighting the complexity of these interactions across environments.

Management and stress tolerance

We did not observe differences in p50 between all managed juvenile ponderosa pines or all unmanaged juvenile ponderosa pines, nor between managed or unmanaged forest sites at any SWUS location. Our findings suggest that while forest management treatments are often aimed at reducing stand density to increase water availability and mediate high temperatures in ponderosa pine forests (Hardage et al., 2022; Sankey and Tatum, 2022), these treatments did not directly impact the physiology of juveniles in this study. Similarly, Kerhoulas et al. (2013) found that density reduction thinning treatments (high, moderate, and low intensity) had no effect on the growth of small ponderosa pines, and the growth of small trees actually decreased in the dry years following thinning – likely due to climate or environmental factors. The efficacy of forest management to promote natural regeneration is highly dependent on timing and duration of treatment, site quality (Wasserman et al., 2022), and local climate conditions (Kerhoulas et al., 2013; Kolb et al., 2020). This suggests that land managers might need to develop site-specific prescriptions, particularly at those with poor quality or shallow soils where water stress could be amplified under drought. Land managers might need to plant on these sites only during unusually wet years to increase the chance of seedling success, however, this could potentially produce more vulnerable trees depending on the stage that stress tolerance develops. It would be ideal for natural regeneration to occur and succeed rather than planting because planted seedlings may be less stress tolerant than their naturally-grown and hardened counterparts (Pinto et al., 2012), although this is inconclusive (McDonald et al., 2009). Southern Nevada might also be a valuable addition to assisted migration programs seeking more drought-tolerant seed sources (Williams and Dumroese, 2013). Our findings also suggest that stress tolerance of juvenile ponderosa pines in much of the Four Corners region is similar despite differences in climate and environmental conditions across locations. This does not diminish the importance of site-specific planning prior to any forest management treatments, but land managers can assume to a certain extent that ponderosa pine forests in this region will have similar futures, and research conducted could be applicable across the larger area. Our results suggest that while thinning treatments aimed at achieving low or intermediate basal areas are likely to promote greater ponderosa pine regeneration (Flathers et al., 2016; Wasserman et al., 2022), these treatments likely do not directly impact the development of older juveniles.

Acclimation, adaptation, or environmental control?

Age-related differences in water use efficiency, management requirements, and growth (Irvine et al., 2004; Knapp and Soulé, 2011; Kerhoulas et al., 2013; Hankin et al., 2019; Zhang et al., 2022) suggest that juvenile and adult ponderosa pines cannot be considered the same physiologically. The association between height and juvenile p50 across locations suggests that hydraulic vulnerability increases as trees grow larger or age, which has been corroborated by several others across species and ecosystems (López et al., 2016; Courveur et al., 2018; Olson et al., 2018). The finding that juveniles are more stress tolerant than adults could mean that ponderosa pine seedlings have even lower p50 values than juveniles, and that plasticity in stress tolerance is highest during the most vulnerable life stages. However, the relationship between height and p50 was significant only when southern Nevada juveniles were removed and while we did not identify a significant relationship at this location, taller juveniles in southern Nevada typically had less negative p50 values. This opposite response suggests southern Nevada juveniles might retain stress tolerance with age, and we propose three potential pathways – (1) individual acclimation, (2) population- or individual-level adaptation, or (3) environmental control. While variation in hydraulic vulnerability of juvenile ponderosa pines across environments has not been previously identified, our results echo those of López et al. (2016) who found that Mediterranean species *Pinus canariensis* displayed plasticity in cavitation resistance only at the driest provenance. While the construction of a more cavitation-resistant xylem is costly to developing trees, Brodribb et al. (2014) suggests this adaptation is most effective for survival in water-limited ecosystems. Drought conditions have been shown to trigger phenotypic plasticity in ponderosa pine seedlings (Kolb et al., 2016) – particularly at hot, dry sites with strong summer droughts (de la Mata et al., 2022) comparable to southern Nevada. An adaptation and/or acclimation component to stress tolerance could be useful in predicting regeneration success and failure across subregional locations yet would require better understanding of how tolerance develops and varies under different climate and environmental conditions.

The third possibility is that there is no adaptation and/or acclimation involved, and environmental conditions simply killed off less negative p50 juveniles during prolonged dry periods. Petrie et al. (2023) found that natural regeneration failures have been occurring at this location for the approximately 20 years due to the inability for climate to support seedling success. Therefore, juveniles remaining on these sites likely germinated ∼20 to 30 years ago when climate conditions were more favorable for tree establishment. It could be that poor site quality amplified the amount of stress juveniles experienced, eventually leading to mortality of individuals with low vigor or those poorly positioned within the environment (e.g., juveniles growing on a steep slope, in direct sun, or in a dense patch of trees). Perhaps short periods of stress could encourage lower p50 values of developing seedlings and juveniles, and management treatments could be used to supplement weaker trees who would normally die because of high stress. The success of natural regeneration at this location might require intensive management of forest conditions and monitoring climate pulses.

Conclusion

We measured the hydraulic vulnerability of juvenile (~20-30 years old) ponderosa pines growing in 6 climatically-varying locations of the SWUS and evaluated how seasonal climate, environmental conditions, and tree growth (height and diameter) were associated with differences in vulnerability. We found that juvenile and adult ($>$ 50 years old) ponderosa pines had significant differences in p50, suggesting that hydraulic vulnerability varies between stages of tree development. Juvenile ponderosa pines in southern Nevada had more negative p50 values than juveniles in southern Colorado, southern New Mexico, and central Arizona. Compared to all other SWUS locations, southern Nevada also had significantly more severe warm season (April-September) meteorological moisture deficit, lower cool season (October-March) and warm season ψ_p, and lower soil water holding capacity. Thus, lower soil ψ_p, imparted by low warm season precipitation and physical soil characteristics, was associated with higher stress tolerance found in juvenile ponderosa pines growing in southern Nevada. We also found that vulnerability to embolism increases with height in juveniles, an association previously limited to adult trees. While our findings appear to be geographically limited to southern Nevada, these results could provide valuable insight into the future of SWUS ponderosa pine forests under warmer and drier climate conditions. Site quality, specifically soil properties, will play a major role in mediating how climate change impacts stress tolerance of ponderosa pines across the region. Despite associations between climate and environmental characteristics, the reason for higher stress tolerance in southern Nevada juveniles is unclear. 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. Forest vulnerability to novel climate conditions and disturbance may depend on how species and individuals can withstand stress, and those with greater tolerance and plasticity have better chance to regenerate and persist in increasingly arid environments.

CHAPTER 3

EXPLORING BACKGROUND MORTALITY OF PINYON PINE ACROSS DIVERSE CLIMATE AND ENVIRONMENTAL CONDITIONS IN THE SOUTHWESTERN UNITED STATES

Chapter abstract: Drought-induced mortality has been the forefront of pinyon pine research for the past two decades, yet it is unclear how mortality differs in the absence of major disturbance - particularly across different climate and environmental conditions, and between or among pinyon species. I used the Cox Proportional Hazards (PH) model to evaluate background mortality hazard for adult pinyon pines in three climatically-varying locations (Colorado, Arizona, and Nevada) of the southwestern United States (SWUS). Life status (living/dead) and tree size were recorded for *Pinus edulis* (Colorado pinyon; Colorado, Arizona) and *Pinus monophylla* (single-leaf pinyon; Nevada) over multiple 10-year periods from 2001-2019 (USFS FIA). I then contrasted the climate and environmental conditions of each location using gridded meteorological estimates (DayMet) and soil simulations (POLARIS). My objectives were to determine if background mortality varied between adult pinyon pines growing in different subregional locations over a 10-year period, and to analyze driving factors and their potential time-dependent effects for *P. edulis* and *P. monophylla*.

10-year background mortality ranged from 4-6% across locations and was lower than previously reported for *P. monophylla*. Adult *P. edulis* in Arizona had the greatest cumulative hazard and lowest overall survival probability over a 10-year period. Based on my results, factors influencing background mortality varied between study locations. The probability of mortality significantly

decreased with greater cool and warm season precipitation, % soil organic matter (30-100 cm), and % soil silt content (100-200 cm; $p < 0.05$). The probability of mortality significantly increased with greater tree size (height and diameter), soil pH (30-100 cm), and cool season maximum air temperature ($p < 0.05$). My results show that the mechanisms driving background mortality in adult pinyon pines differ between and among species occupying different climate regimes, and provide further evidence that tree size increases pinyon pine mortality risk.

Introduction

Pinyon pines are one of the most widely distributed conifers in the southwestern United States (SWUS), encompassing millions of hectares of woodlands, shrublands, and savannas throughout the region (West, 1999; Romme et al., 2009). This wide geographic range results in high variability of seasonal climate and soil physical properties across different environments (Cole et al., 2008). Pinyon pine distribution is largely influenced by the timing and frequency of precipitation, and species occupy different ecological niches shaped by seasonal precipitation patterns (Cole et al., 2008; 2013). Precipitation and temperature in the SWUS differ latitudinally - southern latitudes have higher temperatures and greater warm-season precipitation, and northern latitudes have milder temperatures and are dominated by cool-season precipitation (Jones and Gutzler, 2016). Precipitation and temperature can also fluctuate seasonally under the North American monsoon, where a change in wind patterns brings high rainfall and cooler temperatures in the warm season that can persist from years to several decades (Adams and Comrie, 1997; Guirguis and Avissar, 2008). Climate conditions can also vary at much smaller scales with differences in topography and elevation throughout the landscape (Sheppard et al., 2002; Koehn et al., 2021). Further, soil and edaphic properties translate how climate conditions are received by plants through soil texture and composition, infiltration, and water-holding capacity (Bales et al., 2011; Bradford et al., 2019; Duniway et al., 2019). In addition to biophysical differences, variation in species composition, stand structure, human management, and disturbance further contribute to the heterogeneity observed in pinyon pine (Romme et al., 2009; Williams et al., 2018). The structure and composition of pinyon pine communities are influenced by weather (short-term) and climate (long-term) variation, which can alter seed production, establishment, and mortality rates (Betancourt et al., 1993; Greenwood and Weisburg, 2008; Flake and Weisburg, 2019). Insect infestation (Santos and Whitham, 2009; Gaylord et al., 2013), wildfire (Rodman et al., 2022), and drought (Breshears et al., 2008; Clifford et al., 2013; Macalady and Bugmann, 2014) are common disturbances affecting pinyon pine, and frequent or simultaneous disturbances can exacerbate stressful conditions, which often vary from one location to the next (Anderegg et al., 2015a). Management of pinyon pine often consists of density-reduction thinning, prescribed burning, or planting - often to improve tree fitness and resilience and to maintain forest cover (Gottfried et al., 2008; Redmond et al., 2023). While environmental variation can act as a buffer to ecological change (De Frenne et al., 2020; Ma et al., 2023), it can add difficulty to tracking changes in forest cover, biomass, and mortality through time.

Tree mortality can be influenced directly or indirectly through interactions between plant physiology, weather, topography, soil characteristics, stand structure, and disturbance (van Mantgem et al., 2009; Taccoen et al., 2021; 2022). Mortality in trees can primarily be seen via two physiologic pathways: 1) hydraulic failure, or 2) carbon starvation (McDowell et al., 2011; Adams et al., 2017). Hydraulic failure occurs when water loss from transpiration is greater than water uptake through the roots, creating high xylem water tension (Sperry et al., 1988). If these conditions persist, cavitation occurs, resulting in a loss of conductivity in the xylem and death over time (Sperry and Tyree, 1988). Larger trees are thought to be more vulnerable to hydraulic failure due to greater metabolic and maintenance costs (Couvreur et al., 2018; Choat et al., 2018). The second is carbon starvation which occurs at a slower rate (Peltier et al., 2023) and is typically a result of prolonged low water conditions or disease (McDowell et al., 2008). When the stomata of a plant close to avoid water loss, photosynthesis is prevented, and death eventually occurs via "starvation" (Sevanto et al., 2014). The amount and timing of cool-season precipitation plays a critical role in this process, where cooler, wetter periods allow trees to recover from water stress and rebuild carbon reserves (Biondi and Rossi, 2015; Redmond et al., 2017). While these processes are believed to be independent of each other, both are tied to the availability of water (Thompson et al., 2023). Tree mortality is also strongly tied to temperature in the SWUS (Allen et al., 2010; McDowell et al., 2016), where warmer temperatures can increase water loss from the soil (Bradford et al., 2019; Cholet et al., 2022), increase plant transpiration rates (Kolb and Robberecht, 1996; Seneviratne et al., 2010), and promote greater insect population sizes (Classen et al., 2005; Berg et al., 2006). There is some disagreement on the role of topographic characteristics such as slope, aspect, and elevation in pinyon pine mortality, however, it is widely accepted that fine-scale differences in precipitation and temperature associated with topography are significant (Meddens et al., 2015). Peterman et al. (2013) found that tree mortality was associated with low water-holding capacity due to differences in soil texture and depth among sites, which can vary across relatively short spatial scales (Famiglietti et al., 2008). The effects of soil properties may vary through time as precipitation regimes are expected to be altered under climate change (Bradford et al., 2020). Plants growing on coarse-textured soils are believed to experience less water stress than plants on fine-textured soils, and this relationship may differ with annual precipitation (Noy-Meir, 1973). The availability of soil water is also largely dependent on tree density, and competition can reduce the efficiency of tree growth during periods of favorable conditions in *Pinus edulis* (Macalady and Bugmann, 2014). Mortality in trees inevitably depends on the duration and intensity of stressful conditions (Falk et al., 2022), and the level of stress an individual can tolerate due to factors such as age/size (Ogle et al., 2000; Stovall et al., 2019) or position in the landscape (Paz-Kagan et al., 2017; Taccoen et al., 2022). Much recent work has focused on disentangling the mechanisms contributing to pinyon pine mortality in response to severe disturbance, particularly drought (Breshears et al., 2008; Clifford et al., 2013; Macalady and Bugmann, 2014) and insect outbreaks (Santos and Whitham, 2009; Gaylord et al., 2013), where an unusually high proportion of tree die-off occurs. Consequently, less effort has been directed towards understanding pinyon pine mortality in the absence of a major disturbance event.

Background mortality in trees is defined as death in the absence of a major disturbance (Das et al., 2016) and while this process occurs at a much smaller magnitude ($>$ 1% to 2%), the effects on forest structure, function, and regeneration can be significant over large time scales (Nagel et. al, 2021). It is understood that variability in disturbance-induced and background mortality act as regulators of change in forest ecosystems (Nagel et al., 2021). Despite this, there is very little information on how this process occurs in pinyon pine. Meddens et al. (2015) found that across 21 studies, pinyon mortality ranged from near 0 to over 95% depending on location, study extent, spatial resolution, and measurement method used. Flake and Weisburg (2019) stated that mortality occurred at 8 times the background rate, and reported 10.9% mortality from 2005-2015 in central Nevada (*P. monophylla*, minor *P. edulis* component). In contrast, Biondi and Bradley (2013) found that *P. monophylla* mortality was $<$10% after the early 2000s drought in mixed conifer forests of southern Nevada. The effects of climate on background tree mortality are mediated by stand and tree-scale factors (Taccoen et al., 2019; 2021), often leading to variation in mortality rates between different species or size/age classes (Nagel et al., 2021). Quantifying patterns of background mortality could be useful for identifying vulnerable areas that might require targeted management, or sites where mortality is outpacing regeneration. Background mortality could incite significant change in composition and structure for vulnerable pinyon stands with few seed sources or those where tree and shrub density are very low (Redmond and Barger, 2013). There is also potential for background mortality rates to vary between and/or within pinyon species similar to observed drought-induced mortality (Ogle et al., 2000; Breshears et al., 2008; Macalady and Bugmann, 2014; Gaylord et al., 2015).

Analyzing pinyon pine mortality at the individual level could provide insight into why mortality differs so broadly across locations in the SWUS. Recent evidence has shown that *P. monophylla* and *P. edulis* are genetically distinct species and have evolved within different ecological niches (Buck et al., 2023), believed to be driven by summer monsoon rainfall (Cole et al., 2008; Romme et al., 2009). *P. monophylla* is found primarily in the Great Basin, where a majority of the annual precipitation falls in the cool season as snow at higher elevations and rainfall at lower elevations (Miller et al., 2005; Williams et al., 2018). *P. edulis* is found at higher elevations throughout the SWUS, and sites are typically dominated by summer monsoon rainfall (Williams et al., 2018). Differences in the role of precipitation and temperature across pinyon pine species highlights the potential for background mortality to vary under predicted climate change. Trees occupying arid sites may be more vulnerable to mortality due to lower carbon assimilation and reserve that aid in metabolism, growth, and defense (McDowell et al., 2008), greater temperature and precipitation extremes (Shriver et al., 2022), or soils with low water holding capacity (Bradford et al., 2020). Other authors argue that trees in drier sites might have lower mortality risk, and periods of tolerable stress could promote greater resistance to disturbances such as drought or insect infestation in pinyon pine (Whipple et al., 2019). In contrast, trees occupying wetter sites could be prone to greater mortality because local adaptation may promote lower below- and above-ground biomass (Vasey et al., 2023), fewer defensive structures (Wimmer and Grabner, 1997), or vulnerable hydraulic architecture (McDowell et al., 2008) that reduce stress tolerance. Severe disturbances such as drought are selective in nature (Ogle et al., 2000), and trees that survive periods of elevated stress could promote greater plasticity of growth traits (Kozlowski and Pallardy, 2002; Depardieu et al., 2020). Genetic and trait features may allow for pinyon pines occupying range edges to survive selective drought events due to greater hybridization and adaptation potential (Buck et al., 2023). Evaluating background mortality rates across climate and environmental gradients could aid in understanding differences in forest resilience and recovery when disturbance does occur.

Studies investigating the climate- and environmentally-driven processes of background mortality are relatively uncommon in pinyon pine. I present the results from 12,047 adult pinyon pines located on USFS Forest Inventory and Analysis (FIA) plots across three climatically varying locations in the SWUS - Colorado, Nevada, and Arizona. I also document background mortality rates at each location for a total of 1,348 pinyon pine saplings. My objectives were to: 1) determine if adult pinyon pine background mortality differs over a 10-year period in climatically varying locations of the SWUS, 2) analyze associated variables and their potential time-dependent effects for *P. edulis* and *P. monophylla*, and 3) document 10-year background mortality rates for pinyon pine saplings. *P. monophylla* is believed to be well-adapted to dry conditions (Hartsell et al., 2020; Buck et. al, 2023; Vasey et al., 2023), and is shown to have lower mortality rates compared *P. edulis* (Biondi and Bradley, 2013). Therefore, I hypothesize that locations containing mostly *P. monophylla* will have lower background mortality than those dominated by *P. edulis*. It is well-known that precipitation has a strong influence on pinyon pine distribution (Gray et al., 2006; Cole et al., 2008), regeneration (Minott and Kolb, 2019), growth (Redmond et al., 2017), and mortality (Clifford et al., 2013), and these relationships vary between pinyon species. I hypothesize that background mortality will have the strongest association with seasonal precipitation, particularly cool-season precipitation for *P. monophylla* and warm-season precipitation for *P. edulis*. Young conifers are believed to be more vulnerable due to limited capacity to acclimate growth across different environments (Pirtel et al., 2021). Therefore, I hypothesize that pinyon pine sapling mortality will be higher than adults. This study fills a critical gap in pinyon pine research, where much of the research on mortality is focused on the occurrence of extreme mortality events (Meddens et al., 2015; Hartsell et al, 2020).

Site Description

My study locations covered a range of climate conditions in the SWUS (Figure 3.1), however, information regarding forest structure, species composition, topography, soil and edaphic properties, disturbance, and forest management is limited. The area of study encapsulated 12,047 pinyon pines across Colorado, Nevada, and Arizona (Table 3.1), and successfully captured regional variation in cool and warm season meteorological conditions such as precipitation, temperature, and solar radiation ($p < 0.05$, ANOVA; Table 3.2).

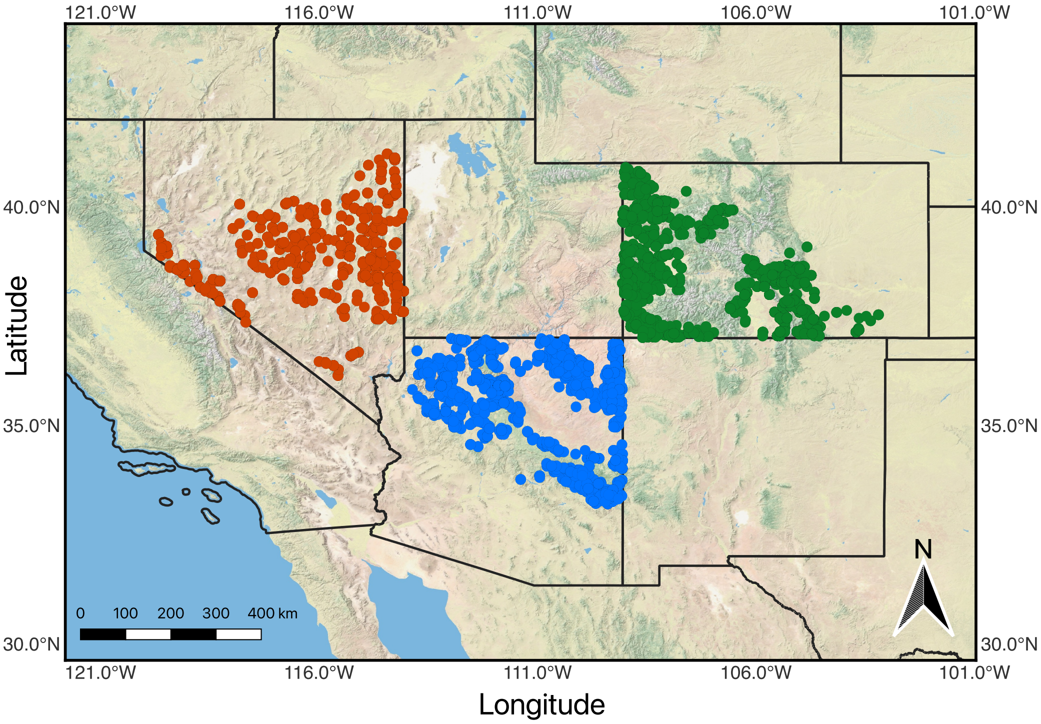


Figure 3.1: Map of southwestern US study locations, points represent individual adult pinyon pines.

Table 3.1: Growth and plot attributes of sampled adult pinyon pines ($\bar{x} \pm$ one standard deviation) at each location. Plot attributes include stocking (plot basal area relative to optimum plot density) and elevation [m]. Growth attributes include initial and 10-year measurements of tree height [m] and diameter at breast height [DBH: cm]. No. of censored adults are those who did not experience a mortality event during the 10-year study period, No. of dead trees are those who died during the 10-year study period, and total is the sum of these. Mortality rate is calculated as the number of dead trees divided by the number of total trees * 100.

Variable	Colorado	Nevada	Arizona
Initial Height [m]	5.00 ± 1.57	5.00 ± 5.33	5.90 ± 2.05
10-year Height [m]	5.33 ± 1.56	5.28 ± 5.49	6.17 ± 2.07
Initial DBH [cm]	22.98 ± 9.13	23.97 ± 3.72	22.42 ± 8.35
10-year DBH [cm]	23.63 ± 8.89	24.67 ± 3.61	22.96 ± 8.20
Stocking	2.79 ± 2.80	2.93 ± 3.15	3.11 ± 2.87
Elevation [m]	2196	2198	2043
No. of Censored Adults	4097	2845	4483
No. of Dead Adults	259	123	240
Total Trees	4356	2968	4723
Mortality Rate	6%	4%	5%

Seasonal precipitation [P: mm] in Arizona is typically bi-modal with higher, monsoon-derived rainfall in the summer (Sheppard et al., 2002). Locations in Colorado received seasonally consistent P and a short, early-summer dry period in the southern portion of the state (Mahoney et al., 2015). Nevada is cooler and wetter on average in the north while southern Nevada is hot and dry, and both are dominated by cool-season P regime (Pan et al., 2011). Based on daily meteorological estimates (DayMet; Thornton et al., 2022), mean annual P at our study sites reached a low of 142 mm in the warm season and a high of 206 mm in the cool season (Table 3.2). Mean daily air temperature [T_a: °C] ranged from -3°C in the cool season and 25°C in the warm season (Table 3.2).

Table 3.2: Cool (OM: October-March) and warm (AS: August-September) season meteorological estimates (± one standard deviation) for sites in Colorado, Nevada, and Arizona including mean annual precipitation [P: mm], daily minimum [T_a min: °C] and maximum air temperature [T_a max: °C], and mean daily solar radiation [SR: MJ/m^2/day] (DayMet; Thornton et al., 2022). Letters indicate statistically different means, determined by ANOVA and Tukey's honest significant difference tests ($p < 0.05$).

Variable	Colorado	Nevada	Arizona
OM P [mm]	$182 \pm 52.3_c$	$206 \pm 57.0_a$	$185 \pm 46.8_b$
OM T_a min [°C]	$-5.91 \pm 1.62_c$	$-4.87 \pm 1.29_b$	$-3.02 \pm 1.68_a$
OM T_a max [°C]	$8.17 \pm 1.74_b$	$7.98 \pm 1.34_c$	$11.38 \pm 1.61_a$
OM daily SR [MJ/m^2/day]	$11.9 \pm 0.822_b$	$11.3 \pm 0.580_c$	$12.5 \pm 0.602_a$
AS P [mm]	$243 \pm 52.0_a$	$142 \pm 41.3_c$	$180 \pm 52.5_b$
AS T_a min [°C]	$7.14 \pm 1.83_b$	$6.71 \pm 1.43_c$	$8.81 \pm 1.47_a$
AS T_a max [°C]	$23.4 \pm 1.82_b$	$22.0 \pm 1.68_c$	$25.2 \pm 1.33_a$
AS daily SR [MJ/m^2/day]	$22.5 \pm 0.602_b$	$23.1 \pm 0.528_a$	$23.1 \pm 0.425_a$
Years Measured	2002-2019	2004-2016	2001-2019

Pinyon pine stand structure throughout the SWUS varies with soil moisture and the amount and timing of precipitation, but typically exists within three broad categories: 1) persistent woodlands, 2) wooded shrublands, or 3) savannas (Romme et al., 2009). *P. monophylla* and *P. edulis* are often found co-dominating stands with *Juniperus osteosperma* (Utah juniper) and *Juniperus scopulorum* (Rocky mountain juniper; Abella et al., 2012; Witt et al., 2022). Other common plant associations include several types of grasses and shrubs, which vary in density and composition depending on habitat conditions (Romme et al., 2009). Elevation across study sites averaged 2043-2198 m across locations (Table 3.2). Soil texture and composition vary spatially across the SWUS, and can have significant impacts on pinyon pine regeneration (Minott and Kolb, 2020) and growth (Whipple et al., 2019). Some variation in soil texture across locations can be seen in this study (Table 3.3).

Table 3.3: Mean soil and edaphic properties for sites in Colorado, Nevada, and Arizona including % clay, silt, sand, and organic matter [OM], soil pH, residual soil water content [θ_r: m^3 m^{-3}], and saturated soil water content [θ_s: m^3 m^{-3}] from 0-200 cm soil depths (POLARIS; Chaney et al. 2019).

Variable	Colorado	Nevada	Arizona
Clay [%] 0-30 cm	18.1 ± 5.46	20.1 ± 7.40	19.3 ± 7.43
Clay [%] 30-100 cm	20.5 ± 7.85	24.0 ± 10.5	23.0 ± 10.5
Clay [%] 100-200 cm	16.8 ± 6.39	15.1 ± 6.17	18.4 ± 7.78
Silt [%] 0-30 cm	29.4 ± 7.26	32.8 ± 6.92	29.6 ± 10.0
Silt [%] 30-100 cm	25.3 ± 10.3	26.7 ± 6.96	26.3 ± 11.8
Silt [%] 100-200 cm	22.8 ± 12.5	22.2 ± 8.21	20.9 ± 10.4
Sand [%] 0-30 cm	49.1 ± 11.0	40.2 ± 9.84	50.4 ± 15.3
Sand [%] 30-100 cm	49.5 ± 14.7	43.2 ± 11.1	49.1 ± 16.8
Sand [%] 100-200 cm	53.9 ± 14.1	53.9 ± 13.5	53.0 ± 16.4
pH 0-30 cm	7.20 ± 0.61	7.37 ± 0.54	7.39 ± 0.52
pH 30-100 cm	7.55 ± 0.61	7.55 ± 0.53	7.56 ± 0.44
pH 100-200 cm	7.66 ± 0.54	7.62 ± 0.60	7.74 ± 0.39
OM [%] 0-30 cm	1.53 ± 1.27	1.59 ± 0.94	1.39 ± 0.80
OM [%] 30-100 cm	0.42 ± 0.30	0.61 ± 0.34	0.52 ± 0.38
OM [%] 100-200 cm	0.14 ± 0.13	0.21 ± 0.21	0.25 ± 0.31
θ_r [m^3 m^{-3}] 0-30 cm	0.06 ± 0.01	0.06 ± 0.02	0.06 ± 0.02
θ_r [m^3 m^{-3}] 30-100 cm	0.06 ± 0.02	0.06 ± 0.02	0.06 ± 0.03
θ_r [m^3 m^{-3}] 100-200 cm	0.05 ± 0.02	0.04 ± 0.01	0.06 ± 0.02
θ_s [m^3 m^{-3}] 0-30 cm	0.49 ± 0.03	0.51 ± 0.03	0.49 ± 0.03
θ_s [m^3 m^{-3}] 30-100 cm	0.47 ± 0.03	0.50 ± 0.03	0.47 ± 0.03
θ_s [m^3 m^{-3}] 100-200 cm	0.46 ± 0.03	0.47 ± 0.03	0.46 ± 0.02

Disturbances such as insect attack (Santos and Whitham, 2009; Gaylord et al., 2013), wildfire (Rodman et al., 2022), and drought (Breshears et al., 2008; Clifford et al., 2013; Macalady and Bugmann, 2014) are often reported in SWUS pinyon pines. Here, I excluded sites disturbed by wildfire to avoid confounding effects on mortality risk. The leading cause of disturbance across locations was insect attack (Figure 3.2), estimated visually by FIA field crews. Common management treatments for SWUS pinyon pines include density-reduction thinning, prescribed burning, fuel-reduction treatments, and tree planting which often aim to improve forest resilience, promote tree growth, and encourage tree regeneration following disturbance (Redmond et al., 2022). Information regarding forest management for locations in this study was unavailable. In this study, I include to two main pinyon species in the SWUS, *Pinus edulis* (Colorado pinyon) and *Pinus monophylla* (single-leaf pinyon).

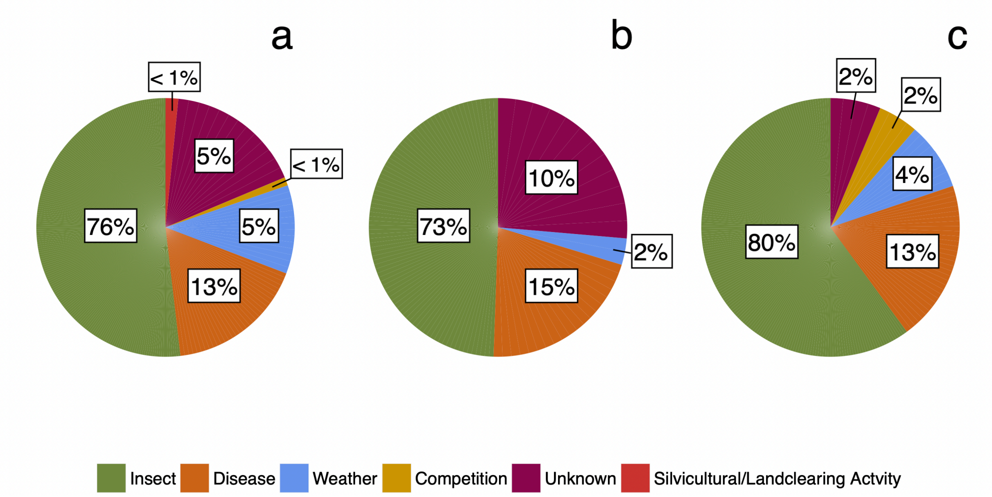


Figure 3.2: Pie charts illustrating estimated disturbance agents for adult pinyon pines in Colorado (Panel a, n = 259 dead), Nevada (Panel b, n = 123 dead), and Arizona (Panel c, n = 240 dead), as determined by FIA field crews.

Methods

USFS Forest Inventory and Analysis data

Raw tree (TREE) and plot (PLOT) characteristic tables were downloaded from the United States Forest Service (USFS) Forest Inventory and Analysis (FIA) DataMart (https://www.fs.usda.gov/research/products/dataandtools/tools/fia-datamart) for Colorado, Nevada, and Arizona in June 2023. These locations were chosen because FIA sampling intervals were consistent throughout the study period – trees were sampled initially and re-sampled at least once within a 10-year period. Data tables were then filtered by species (SPCD) to contain only adult (> 12.7 cm diameter) *P. edulis* (Colorado, Arizona) and *P. monophylla* (Nevada) observations. Average initial diameter [cm] of adult pinyon pines ranged ∼22-24 cm across locations, and average initial height [m] was 5-6 m (Table 3.1). 10-year cohorts were created using the previous (PREV_STATUS_CD) and current status code (STATUSCD; 1 = living, 2 = dead) for each tree from 2002-2019 in Colorado (8 cohorts), 2004-2016 in Nevada (3 cohorts), and 2001-2019 in Arizona (9 cohorts). If trees were not re-sampled within a 10-year period, they were removed from the analysis. Mortality year (MORTYR) and disturbance agent (AGENTCD) were estimated by FIA field crews. Trees that were damaged or killed by wildfire were removed from the sample. Also, trees that were sampled via remote sensing or modeling were removed in order to prevent further uncertainty in the data.

Meteorological estimates and soil simulations

Meteorological variables in my analyses included daily P, minimum [T_a min: °C] and maximum [T_a max: °C] air temperature, and I report daily solar radiation [SR: $MJ/m^2/day$] to further characterize sites (Table 3.2). Meteorological variables were derived from Oak Ridge National Laboratory DayMet gridded meteorological estimates (Thornton et al., 2022), at a 1 km^2 resolution [https://daymet.ornl.gov/]. Meteorological variables were evaluated over two seasonal time periods: warm season (AS: April-September) and cool season (OM: October-March).

I derived soil simulations [% gravel, % sand, % clay, % organic matter, pH, residual water content, θ_r: m^3 m^{-3}, and saturated water content, θ_s: m^3 m^{-3}] from probabilistic soil properties database POLARIS (Chaney et al., 2019). Estimates were given at varying incremental depths ranging 0-200 cm. I averaged all variables to incremental depths of 0-30 cm, 30-100 cm, and 100-200 cm and report the mean of each location (Table 3.3).

Cox Proportional Hazards Model

To explore pinyon pine mortality risk at the individual level, I used the Cox Proportional Hazard (PH) model (Cox, 1972). The model is essentially a regression model that is often used in a medical studies to investigate relationships between patient survival time and one or multiple predictor variables. Previous studies in trees have shown that the Cox PH model can be an effective tool for modeling tree mortality (Maringer et al., 2021, Uzoh and Mori, 2012). The Cox PH model allows survival time to be described as a function of several predictor variables. Unlike other survival analyses, the Cox PH model can handle categorical and continuous variables. The model equation is as follows:

$$h(t) = h_0(t) \times exp(b_1x_1 + b_2x_2 + ... + b_nx_n) \tag{3.1}$$

where t is time, h(t) is the hazard function, h$_0$(t) is the baseline hazard function, which is described as a non-negative function of time, and b$_1$x$_1$, b$_2$x$_2$ and b$_n$x$_n$ represent the predictor variables. This produces a hazard ratio (HR), which is the proportion of the total number of observed to expected events between the two groups, in this case dead and surviving trees. The HR is computed from all observations in the survival curve and assesses how quickly an individual experiences the event of interest. A HR > 1 represents an increase of hazard risk, HR < 1 represents a decrease of hazard risk, and a HR $= 1$ represents no change in hazard risk between the two groups. Time to event is the amount of time an individual survives prior to or, in absence of the desired event – which in this case event was mortality. Time to event was calculated as the difference between the initial measurement year and the estimated mortality year for each tree. Trees who did not die within the 10-year period were right-censored in the analysis (Kalbfleisch and Prentice, 1980). This process does not remove observations from the model.

A cluster term was implemented in each model to correct for correlated observations. Clustering is used to compute robust variance for each term and cluster ID, in this case the cluster term was site. If the site is not unique, the observation will cluster with correlated sites. It is important to note that we did not stratify the model by site, which produces a separate baseline hazard for each site, due to the coarseness of the dataset. Cox PH models were fitted separately for adult pinyon pines in Colorado, Nevada, and Arizona. All three Cox PH models were fitted with tree status (dead/alive) and time to mortality in years as the response variable. Explanatory variables were first fitted in the Cox PH separately. Significant variables were then added to the models with respect to the degrees of freedom and number of mortality events. It is generally a rule of thumb to have 10-15 event observations per variable when using the Cox PH model to preserve predictive power and accuracy (Concato et al., 1995) Lastly, initial non-significant variables were added back into the model order to confirm or reject statistical significance. This process was repeated for three separate models at each study location, with different sets of predictor variables: ”climate” (meteorological estimates only), ”soil” (soil and edaphic properties only), and ”mixed” (various combinations of the two). Models also contained tree characteristics such as tree size when significant. The model fit was assessed by comparing the Akaike information criterion (AIC; Akaike,

1973) and analyzing model deviance, concordance, and residuals, such as Cox-Snell (Cox and Snell, 1968), scaled Schoenfeld (Grambsch and Therneau, 1994), and Martingale (Therneau, 1990), of the covariates. All covariates included in the model indicated that the proportional hazards assumption was met. The model with the lowest AIC value was chosen. Relative hazard is defined as the ratio of hazard at time t and the baseline hazard ($\mathrm{h}_0(t)$) to risk factors. Here, I use rank-hazard plots that incorporate relative hazard to investigate of how different values of the covariate present in the data influence hazard risk.

Statistical Analysis

I used R statistical software (R Core Team, 2023) for all data cleaning/formatting, statistical analyses, and figures. The R package *survival* (Therneau, 2024) was used to run the Cox PH model. DayMet meteorological estimates (Thornton et al., 2022) were batch downloaded using the *daymetr* R package (Hufkens et al., 2018). POLARIS soil simulations (Chaney et al., 2019) were batch downloaded using the *XPolaris* R package (archived; Moro Rosso et al., 2021). The R package *rankhazard* (Karvanen and Harrell, 2009) was used to generate rank-hazard plots.

Results

Individual-based models of background mortality hazard

Arizona had the highest cumulative hazard and lowest overall survival probability over a 10-year period compared to Colorado and Nevada, respectively (Figures 3.2, 3.3).

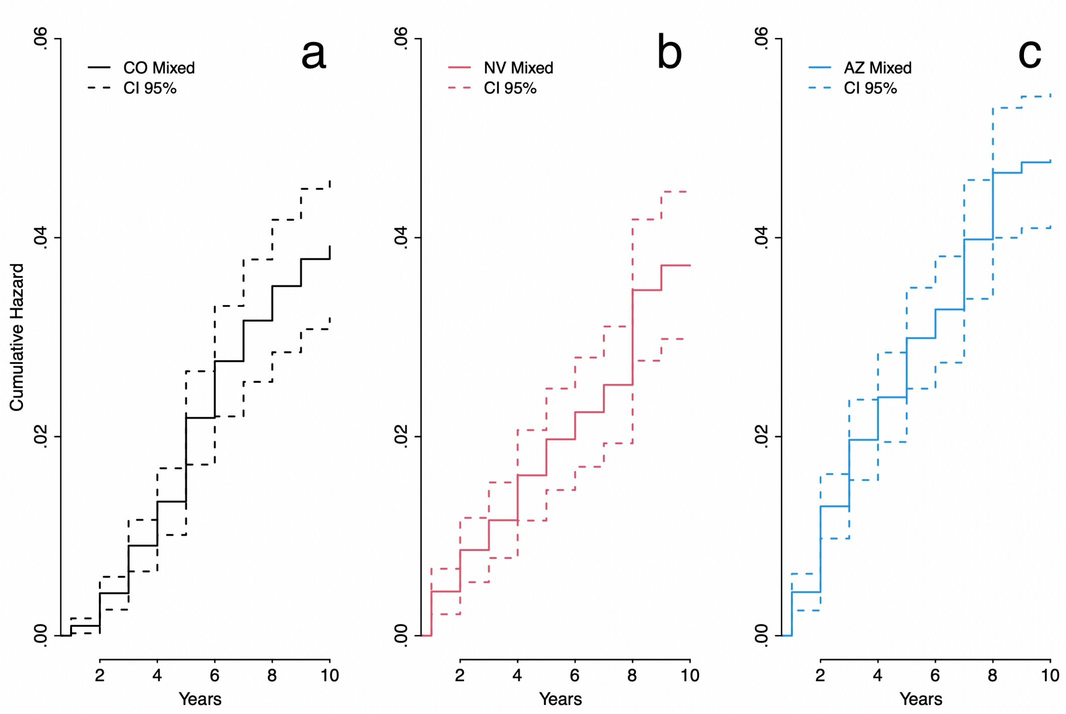


Figure 3.3: Cumulative background mortality hazard over the 10-year study period for adult pinyon pines in Colorado (Panel a), Nevada (Panel b), and Arizona (Panel c). Dashed lines illustrate the 95% confidence interval for each Cox-PH model.

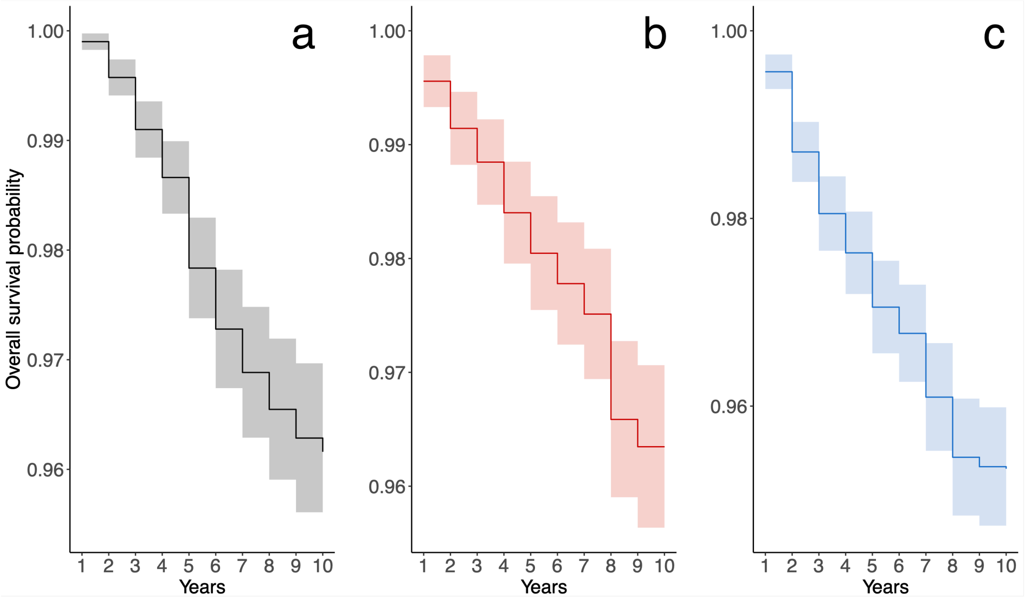


Figure 3.4: Overall survival probability for adult pinyon pines in Colorado (Panel a), Nevada (Panel b), and Arizona (Panel c) over the 10-year study period. Shaded areas illustrate the 95% confidence interval for each Cox-PH model.

The best fitting model of pinyon pine mortality hazard at all 3 locations was the 'mixed' model which included meteorological estimates, soil characteristics, and tree measurements (Table 3.4, 3.5), highlighting the importance of analyzing mortality as a function of both abiotic and biotic interactions. The model with the highest concordance was Colorado (0.747 SE 0.014), followed by Nevada (0.644 SE 0.025), and Arizona (0.599 SE 0.02).

Table 3.4: Cox-PH model covariates, hazard ratios, and p-values for Colorado (CO), Nevada (NV), and Arizona (AZ). Exp(β) is the hazard ratio (HR) where > 1 indicates an increase in mortality hazard, < 1 indicates a decrease in mortality hazard, and 1 represents no change in mortality hazard. Covariates are cool (OM: October-March) and warm (AS: April-September) season mean annual precipitation [P: mm], mean daily minimum [T_a min: °C] and maximum [T_a max: °C] air temperature, % clay, sand, silt and organic matter content from 30-200 cm soil depths, and soil pH 30-200 cm depths. Bold text indicates significance ($p < 0.05$) and — represents non-inclusion in the model.

Covariate	CO Exp(β)	CO p-value	NV Exp(β)	NV p-value	AZ Exp(β)	AZ p-value
OM T_a min [°C]	0.996	0.980	1.03	0.646	—	—
OM T_a max [°C]	**1.33**	**0.000946**	—	—	—	—
AS T_a min [°C]	1.02	0.904	—	—	—	—
AS T_a max[°C]	1.09	0.447	—	—	—	—
OM P [mm]	—	—	—	—	**0.996**	**0.0323**
AS P [mm]	**0.994**	**0.00444**	0.995	0.0940	0.997	0.0880
Clay [%] 30-100 cm	—	—	0.991	0.559	1.02	0.231
Clay [%] 100-200 cm	—	—	1.03	0.151	0.981	0.264
Silt [%] 100-200 cm	—	—	**0.957**	**0.000817**	—	—
Organic Matter [%] 30-100 cm	**0.298**	**0.00609**	—	—	—	—
pH 30-100 cm	**2.02**	**0.00384**	0.713	0.211	1.31	0.116
pH 100-200 cm	0.902	0.655	—	—	—	—
Initial Height [m]	1.06	0.134	**1.11**	**0.0204**	—	—
Initial DBH [cm]	—	—	—	—	**1.02**	**0.0330**

Table 3.5: AIC table of competing Cox-PH models for Colorado (Section A), Nevada (Section B), and Arizona (Section C) where K represents the degrees of freedom, AIC is the information score of the model, δAIC is the difference between the best model and the current model, AIC weight (Wt.) is the proportion of total predictive power of the model set, Cumulative weight (Wt.) is the sum of AIC weights, and LL is the log-likelihood of the model.

A. AIC Table - Colorado

Model Name	K	AIC	δAIC	AIC Wt.	Cumulative Wt.	LL
CO Mixed	9	4128.28	0.00	1.00	1.00	-2055.12
CO Climate	5	4154.23	25.94	0.00	1.00	-2072.11
CO Soil	7	4228.30	100.01	0.00	1.00	-2107.13
B. AIC Table - Nevada						
NV Mixed	7	1943.77	0.00	0.78	0.78	-964.86
NV Soil	4	1946.31	2.54	0.22	1.00	-969.15
NV Climate	2	1955.05	11.28	0.00	1.00	-975.52
C. AIC Table - Arizona						
AZ Mixed	6	3930.93	0.00	0.55	0.55	-1959.46
AZ Climate	2	3931.33	5.13	0.45	1.00	-1963.66
AZ Soil	4	3945.38	19.17	0.00	1.00	-1968.68

Factors influencing pinyon pine mortality in Colorado

Cool season T_a max was associated with a significant increase of 10-year mortality risk for adult pinyon pines in Colorado ($p < 0.05$, Table 3.4). Higher cool season T_a max was associated with a 1.33 times greater mortality risk over a 10-year period (Table 3.4). The lowest relative hazard for cool season T_a max was 3.04 °C, no change in hazard at 7.83 °C, and highest relative hazard at 13.4 °C (Figure 3.4).

Warm season precipitation was associated with a significant decrease of 10-year mortality risk for adult pinyon pines in Colorado ($p < 0.05$, Table 3.4). Higher warm season P was associated with a 0.994 times lower mortality risk over a 10-year period (Table 3.4). The highest relative hazard for warm season P was at 134 mm, no change in hazard at 237 mm, and lowest relative hazard at 554 mm (Figure 3.4).

Additionally, % soil organic matter at 30-100 cm depth was associated with a significant decrease of 10-year mortality risk for adult pinyon pines in Colorado ($p < 0.05$, Table 3.4). Greater % soil organic matter at 30-100 cm depth was associated with a 0.298 times lower mortality risk over a 10-year period (Table 3.4). The highest relative hazard for % soil organic matter at 30-100 cm depth was 0.02%, no change in hazard at 0.39%, and lowest relative hazard was at 2.3% (Figure 3.4).

Lastly, soil pH at 30-100 cm depth was associated with a significant increase of 10-year mortality risk for adult pinyon pines in Colorado ($p < 0.05$, Table 3.4). Higher soil pH at 30-100 cm depth was associated with a 2.02 times greater mortality risk over a 10-year period (Table 3.4). The lowest relative hazard for soil pH at 30-100 cm was 5.6 pH, no change in hazard at 7.6 soil pH, and highest relative hazard at 8.8 soil pH (Figure 3.4).

High warm season P and high soil organic matter at 30-100 cm depth reduced mortality risk more than low soil pH and low cool season T_a max. Conversely, high soil pH and high cool season T_a max increased mortality risk more than low warm season P and low % soil organic matter 30-100 depth (Figure 3.4).

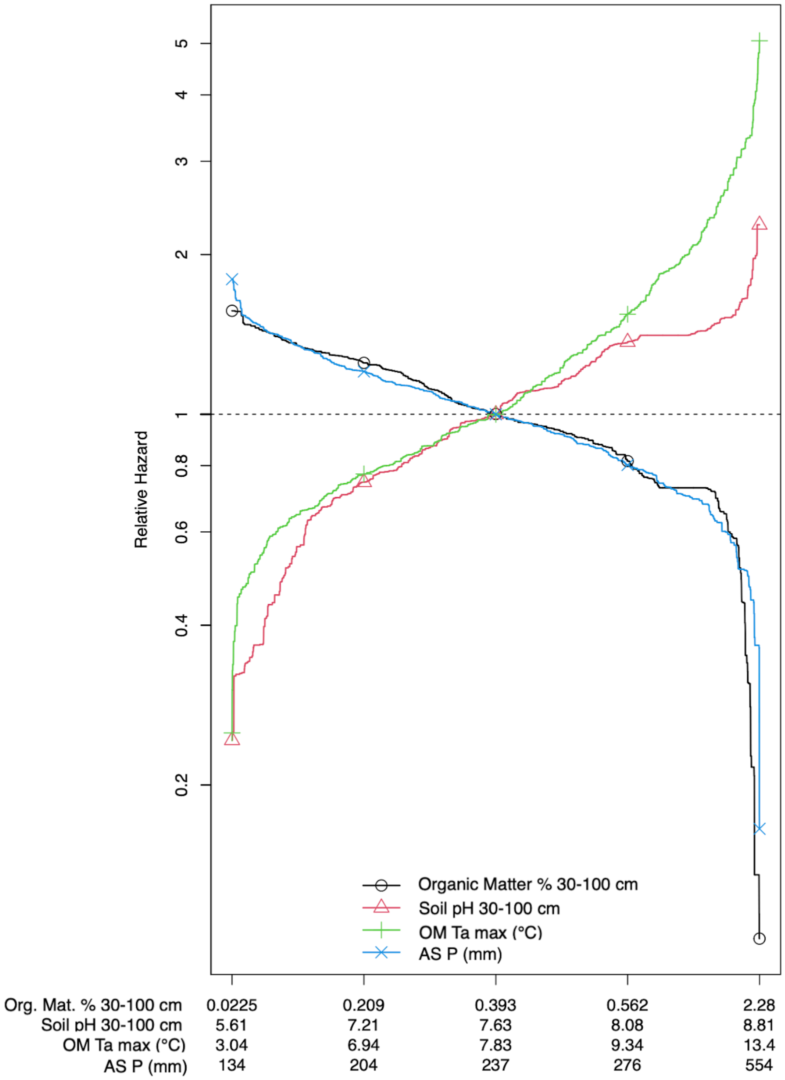


Figure 3.5: Rank-hazard plot illustrating the relative hazard of significant covariates in the Cox-PH model for Colorado. Significant covariates include % organic matter (30-100 cm; black line), soil pH (30-100 cm; red line), cool season (OM) mean daily maximum air temperature [T_a max: °C] (green line), and warm season (AS) mean annual P [mm] (blue line). X-axis is the minimum, 1st QRT, median, 3rd QRT, and maximum values within the data.

Factors influencing pinyon pine mortality in Nevada

Tree height was associated with a significant increase of 10-year background mortality risk for adult pinyon pines in Nevada ($p < 0.05$, Table 3.4). Greater tree height was associated with a 1.11 times higher mortality risk over a 10-year period (Table 3.4). The lowest relative hazard for tree height in Nevada was at 0.91 m, no change in hazard at 4.9 m, and highest relative hazard at 15.5 m (Figure 3.5).

Soil silt content (%) at 100-200 cm depth was associated with a significant decrease of 10-year mortality risk for adult pinyon pines in Nevada ($p < 0.05$, Table 3.4). Higher % soil silt content at 100-200 cm depth was associated with a 0.957 times lower mortality risk over a 10-year period (Table 3.4). The highest relative hazard for soil silt content at 100-200 cm depth was at 0.5%, no change in hazard at 21.1%, and lowest relative hazard at 70.4% (Figure 3.5).

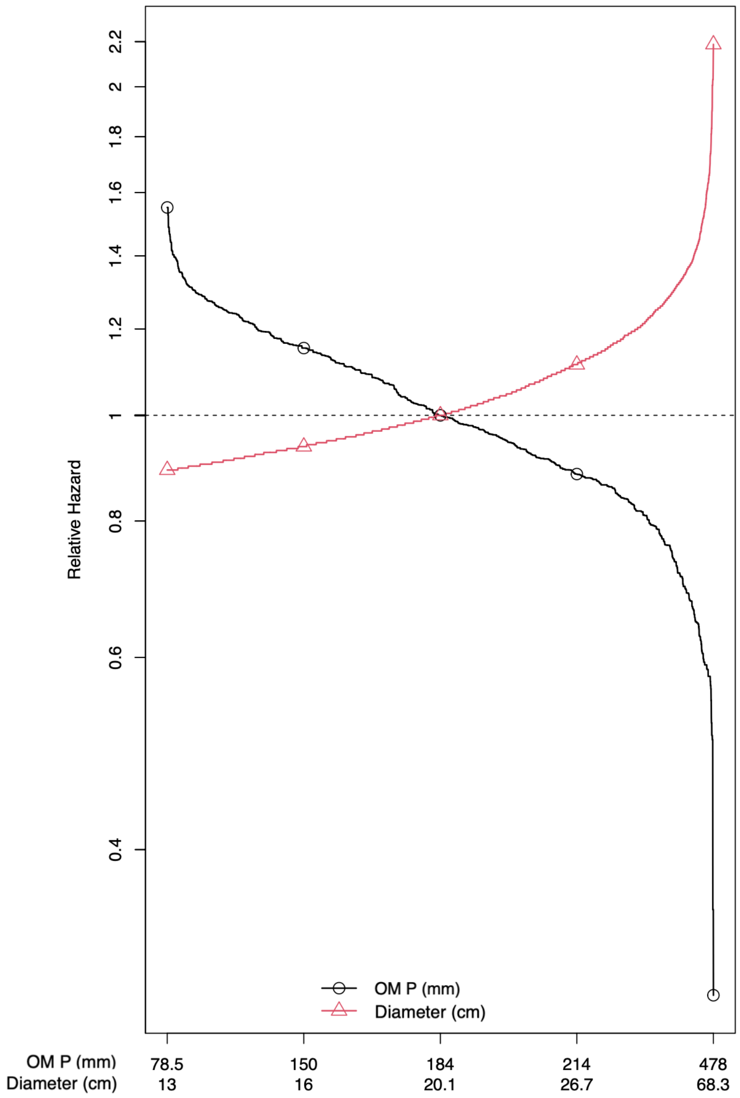


Figure 3.6: Rank-hazard plot illustrating the relative hazard of significant covariates in the Cox-PH model for Nevada. Significant covariates include tree height [m] (black line) and % silt at 100-200 cm soil depth (red line). X-axis is the minimum, 1st QRT, median, 3rd QRT, and maximum values within the data.

Factors influencing pinyon pine mortality in Arizona

Tree diameter was associated with a significant increase of 10-year mortality risk for adult pinyon pines in Arizona ($p < 0.05$, Table 3.4). Larger tree diameter was associated with a 1.02 times greater mortality risk over a 10-year period (Table 3.4). The lowest relative hazard for tree diameter was at 13.0 cm, no change in hazard at 20.1 cm, and highest relative hazard at 68.3 cm (Figure 3.7).

Cool season precipitation was associated with a significant decrease of 10-year mortality risk for adult pinyon pines in Arizona ($p < 0.05$, Table 3.1). Higher cool season precipitation was associated with a 0.996 times lower mortality risk over a 10-year period (Table 3.1). The highest relative hazard for cool season P was at 78.5 mm, no change in hazard at 184 mm, and lowest relative hazard at 478 mm (Figure 3.6).

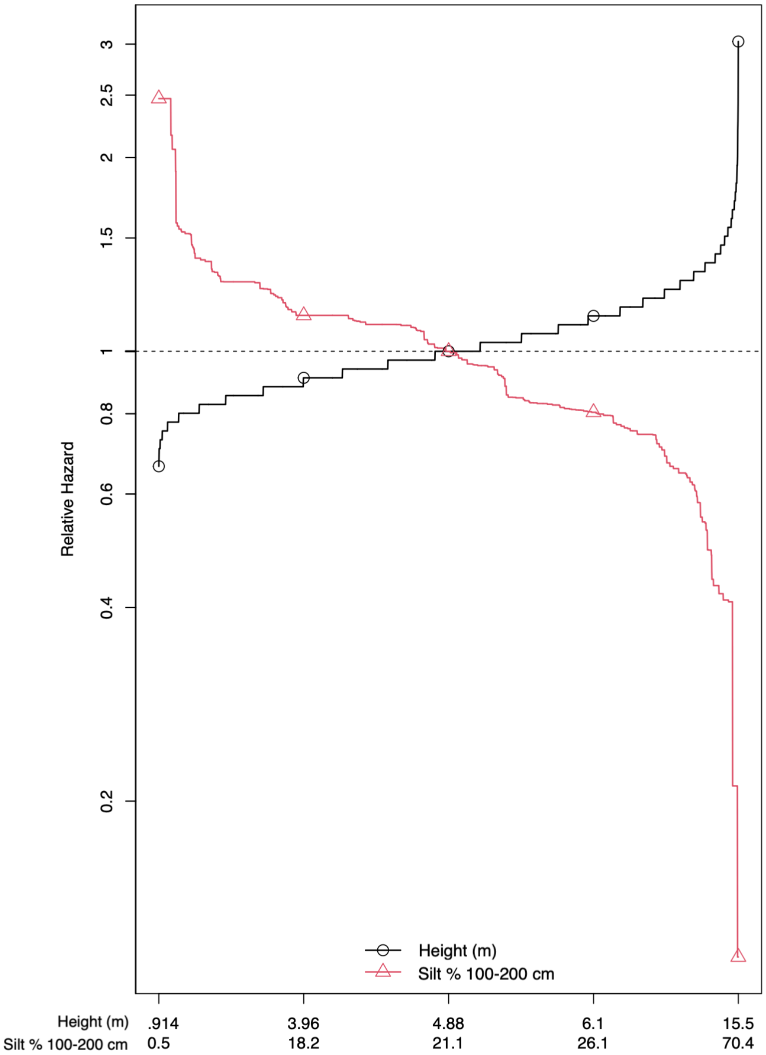


Figure 3.7: Rank-hazard plot illustrating the relative hazard of significant covariates in the Arizona Cox-PH model. Significant covariates include cool season (OM) mean annual P [mm] (black line) and tree diameter [cm] (red line). X-axis is the minimum, 1st QRT, median, 3rd QRT, and maximum values within the data.

Quantifying pinyon pine sapling mortality

Unfortunately, the low number of mortality events in pinyon pine saplings prevented the use of the Cox PH model to investigate factors influencing mortality hazard. In Colorado, 11 out of 466 saplings died from 2002-2019 (2.4%, mortality rate), followed by 1 out of 274 from 2004-2016 (0.4%)

in Nevada, and 11 out of 466 from 2001-2019 (0.8%) in Arizona.

Discussion

In this study, I explored background mortality in adult pinyon pines across three climatically-varying locations of the SWUS, and investigated the climate and environmental variables associated with differences in mortality risk. Due to previous studies suggesting greater tolerance to dry conditions (Hartsell et al., 2020; Buck et al., 2023) and lower mortality in *P. monophylla* (Biondi and Bradley, 2013), I hypothesized that locations containing mostly *P. monophylla* would have lower background mortality than those dominated by *P. edulis*. *P. edulis* in Arizona had the highest cumulative hazard and lowest overall survival probability over a 10-year period, followed by *P. edulis* in Colorado. The 10-year background mortality rate for *P. monophylla* was the lowest out of all three locations at 4% over a 10-year period. This finding suggests that *P. edulis* could be more vulnerable to mortality, even in the absence of a major disturbance. While background mortality is largely unexplored in pinyon pine, this finding is corroborated by Biondi and Bradley (2013) who found that mortality in *P. monophylla* was minimal, and densities of this species increased during periods of widespread mortality in *P. edulis*. Despite this, the lack of information on background mortality in pinyon pine demonstrates that further investigation is needed to determine the validity of this finding for *P. edulis* in other SWUS locations.

In partial support of my second hypothesis, I found that greater warm season precipitation significantly decreased mortality risk for *P. edulis* in Colorado, but not for trees in Arizona. Additionally, precipitation was not the most influential factor governing background mortality for *P. edulis* in Colorado. Instead, I found that factors associated with background mortality could indicate insect attack as a prevalent risk – although confirming this is beyond the scope of this study. Cool season temperature increases and poor soil quality can impact forest health and increase the likelihood of insect infestation. I also found that for pinyon pines in Nevada and Arizona, increased tree size (height, diameter) was associated with greater mortality risk – which is corroborated by other pinyon pine studies (Flake and Weisburg, 2019; Reed and Hood, 2020). This finding suggests that tree growth might be negatively impacted as climate change facilitates local adaptation in areas under frequent water stress. I also documented mortality of pinyon pine saplings within average background mortality range (0.8-2.4%), and these findings indicate that tree age and size are associated with differential survival in pinyon pine.

Spatial variation of abiotic mortality drivers

For adult pinyon pines in this study, the factors influencing background mortality varied across different climate and environmental conditions. It is well-known that precipitation has a strong influence on pinyon pine distribution (Gray et al., 2006; Cole et al., 2008), regeneration (Minott and Kolb, 2019), growth (Redmond et al., 2017), and mortality (Clifford et al., 2013). In partial support of my second hypothesis, precipitation was a significant factor for *P. edulis* in both Colorado and Arizona. *P. edulis* mortality risk was reduced by greater warm season precipitation in Colorado, although it was not the most influential factor, and greater cool season precipitation in Arizona. These findings suggest that drivers of *P. edulis* background mortality in arid locations like Arizona are tightly correlated to the amount and timing of seasonal precipitation, likely due to its importance in recovery and growth following high warm season temperatures (Biondi and Rossi, 2015). It is surprising that *P. edulis* mortality in Arizona lacked association with soil properties because soil and edaphic properties translate climate conditions into soil moisture availability (Liu et al., 2019; Pascolini-Campbell et al., 2019). *P. edulis* mortality in Arizona appears to be more strongly driven by climate in the absence of major disturbance, and differences in environmental conditions at this location might only be apparent during periods of drought where water stress is exacerbated.

In Colorado, the factors influencing adult pinyon pine background mortality were more complex. In more temperate locations, environmental factors such as stand density and resource availability could have a stronger control over tree death. Greater warm season precipitation and soil organic matter decreased the likelihood of mortality in Colorado, while greater soil pH and cool season maximum temperature increased mortality risk. Soil organic matter plays an important role in nutrient availability, and can increase water holding capacity and conductivity between soil layers (Hudson, 1994). In contrast, soil pH can decrease nutrient availability and mobilization, and soil environments with adequate nutrients can reduce the likelihood of disease development (Spann and Schumann, 2009). In pinyon pine, soil pH can be higher under tree canopies and at deeper soil horizons (Everett et al., 1986), and this association could allude to additional negative effects of greater tree densities. Everett et al. (1986) demonstrates that subsurface soil nutrients and pH had significant effects on pinyon pine root distribution and density, and the development of adequate root systems are critical to tree health and survival. In addition to water availability and disease implications, studies have shown that soil nutrients are involved in regulating insect herbivory in forest ecosystems. Conrad-Rooney et al. (2020) found that oak trees in soil with lower nitrogen concentration experienced greater insect herbivory, and that defoliation severity increased with greater inorganic nitrogen content. Soil nutrient concentration can also have an impact on root development, which could explain why soil factors such as pH and organic matter were so influential in the model. Lastly, increases in growing season temperatures can also increase insect population sizes (Classen et al., 2005; Berg et al., 2006). The factors driving mortality in Colorado seem to indicate insects as the main driver of background mortality, highlighting factors that both increase and decrease the chance of infestation – depending on local site conditions.

The influence of soil and edaphic properties on pinyon pine mortality is very apparent in this study.

Soil properties played a significant role in both decreasing and increasing the risk of mortality for adult pinyon pines in Colorado and Nevada. For adult pinyon pines in Nevada, greater soil silt content at 100-200 cm decreased the likelihood of mortality and indicates that trees at this location depend largely on deep soil moisture reserves to avoid mortality. Greater allocation to root development is critical for deep soil moisture access, which could explain the negative effect of tree height at this location. Deep soil moisture plays a critical role in carrying trees through dry periods long after upper soil layers have dried (Szutu and Papuga, 2019). Hubbert et al. (2001) found that by mid-June in Sierra Nevada pine forests, winter snowmelt recharge was depleted in upper layers, and by July plant available water was found exclusively within the fractured bedrock layer. These findings show that the relationship between soil and edaphic properties and mortality is differential across varying climate and environments.

Colorado was the only location where background mortality was predicted to increase with greater temperature, indicating that trees occupying cooler/wetter locations could be disproportionately vulnerable compared to their arid counterparts (Warwell and Shaw, 2018; Whipple et al., 2019; Crockett and Hurteau, 2024). Increases in cool season temperature can reduce pinyon pine cone production (Redmond et al., 2012), and cool season climate conditions determine seedling germination and survival rates (Chambers, 2001). My results show that warm season precipitation, likely driven by the North American monsoon, has the potential to buffer the negative effects of greater cool season temperature on tree mortality. Peltier and Ogle (2018) found that tree growth was negatively affected by longer growing seasons, yet monsoon precipitation acts as a mechanism of recovery following winter drought periods. There is potential for *P. edulis* to be more vulnerable to mortality than *P. monophylla*, particularly in locations with historically favorable climate and weather such as Colorado. As climate forecasts indicate increases in cool season temperature across the SWUS (Bradford et al., 2020), land managers and scientists might see pinyon decline in these areas first due to a lack of conditioning to environmental stress or disturbance, such as those in Nevada and Arizona, where frequent and prolonged periods of perturbations is common.

Size-related influences on background mortality reveal potential for local adaptation

In this study, I demonstrate that tree size (height and diameter) increased background mortality risk for adult pinyon pines in Nevada and Arizona, which is corroborated by several other studies (Mueller et al., 2005; Flake and Weisburg, 2019; Reed and Hood, 2020). This relationship was not identified for adult pinyons in Colorado, indicating that tree size might only be a significant factor when a location experiences more frequent and severe perturbations (Nagel et al., 2021), typically associated with a hot/dry climate regime. Pinyon pine saplings in this study are within normal ranges of background mortality, and this finding shows the potential for size- or age-related differences in background mortality. Larger trees are believed to be more vulnerable to hydraulic failure (Choat et al., 2018) and insect attack (Santos and Whitham, 2009), and the association between tree size and greater mortality in this study highlights the potential for trees to alter their physiologic traits in response to environmental conditions. A paper from Lichtenthaler and Rinderle (1988) described that tolerable stress could activate cell metabolism and physiological activity without causing damage, even over a long periods of time, and this stimuli could be favorable to plant development. Adult *P. monophylla* had the lowest 10-year mortality of all locations in this study, supporting my first hypothesis and the idea that *P. monophylla* might be better adapted to drier conditions than *P. edulis* (Biondi and Bradley, 2013; Hartsell et al., 2020; Buck et al., 2023). Whipple et al. (2019) show that pinyon pines growing under chronic disturbance have greater tolerance to periods of prolonged stress versus those growing in more stable conditions. Greater resilience of trees originating from hot/dry sites has been identified in pinyon and many other tree species (Depardieu et al., 2019; Challis et al., 2021; Fontes et al., 2022; Vasey et al., 2023), and the development of stress-tolerant traits that match local conditions is critical to survival in a changing climate (Alberto et al., 2013). Vasey et al. (2023) demonstrates that while *P. monophylla* seedlings show plasticity to drought conditions, trait variation will likely vary due to differences in localized climate. In a recent paper by Buck et al. (2023), the authors suggest that pinyon pine is well-suited to adapt to changing conditions due to its ability to hybridize with other pinyon species and retain traits that allow for expansion into new, more extreme environments at range edges. These findings highlights the need to better understand how tree mortality responds at different spatial and temporal scales in the SWUS, and how fine-scale differences in climate and environmental conditions impact stress tolerance and adaptation across tree populations (Alberto et al., 2013).

In contrast, Flake and Weisburg (2019) found that taller pinyon pines were less likely to experience mortality in central Nevada. While it is widely accepted that greater tree size increases disturbance-induced mortality in pinyon pine (Meddens et al., 2015), this relationship is inconclusive regarding background mortality. Additionally, there is potential for some warm/dry adapted tree populations to exceed their physiological capacity in the face of climate change (Anderegg et al., 2019). Abella et al. (2015) found that warm slopes experienced the least amount of forest change, and change that occurred was much slower than cooler slopes that shifted rapidly over time. However, the authors also found that warm/dry slopes were the only locations to experience mortality in modern climate conditions, where tree density increased on cooler/wetter sites in comparison. The threshold of stress that an individual can tolerate is tied to the conditions at which they reach physiological equilibrium in their environments. There is growing evidence that life history traits could be just as influential as climate change (Zeng et al., 2020) in modulating mortality and distribution of western US forests (Copeland et al., 2018). These findings reinforce the need for studies that investigate historic and localized patterns of tree mortality which will improve our ability to detect climate change impacts. It is clear that mortality and the factors driving this process differ greatly in pinyon pine (Williams et al., 2018), and there is still uncertainty in predicting and generalizing these patterns across environments.

Quantifying background mortality provides context for extreme mortality events

Establishing a baseline for ecological events can be useful in determining when climate conditions are approaching extreme levels (Smith, 2011). I found that 10-year background mortality was lower than previously reported for *P. monophylla* (Biondi and Bradley, 2013; Flake and Weisburg, 2019), and this study quantified background mortality in *P. edulis*, which is rarely discussed due to the prevalence of drought-induced mortality studies. Relatively small increases in annual background mortality rates, even 0.5%, compounded over several decades can produce similar and potentially greater magnitudes of tree loss compared to major disturbances such as fire and widespread insect infestation (Das et al., 2016). The potential for abiotic and biotic factors to increase tree death in one area might decrease the likelihood of mortality in another, and future works on background mortality should account for localized variation in their analyses.

Conclusion

In this study, I used the Cox Proportional Hazards model to predict background mortality risk to several biotic and abiotic factors for adult pinyon pines in Colorado, Nevada, and Arizona over a 10-year period. I investigated the role of seasonal meteorological variables such as warm and cool season precipitation and air temperature. I also analyzed several soil and edaphic properties such as texture (% sand, silt and clay) and composition (% organic matter), and soil pH ranging 0-200 cm soil depth. Adult pinyon pines in Arizona had the greatest cumulative hazard and the lowest overall survival probability over a 10-year period compared to those in Colorado and Nevada. While insect attack was the leading disturbance in adult pinyon pines across locations (Figure 3.2), I was unable to analyze the relationship between infestation and mortality due to uncertainty in 1) the timing and duration of insect invasion and 2) the level of insect disturbance experienced by surviving trees. In support of my first hypothesis, background mortality was lower at *P. monophylla*-dominated locations compared to those occupied primarily by *P. edulis*. In partial support of my second hypothesis, greater warm season precipitation significantly decreased mortality risk for *P. edulis* in Colorado, but not for trees in Arizona. Additionally, precipitation was not the most influential factor governing background mortality for *P. edulis* in Colorado. While I expected a relationship between cool season precipitation and mortality for *P. monophylla* in Nevada, this association was only identified for *P. edulis* in Arizona. For adult pinyon pines in Colorado, greater mortality risk was observed on sites with higher cool season daily T_a max and soil pH at 30-100 cm depth, and lower mortality risk on sites with greater warm season P and higher percentage of soil organic matter at 30-100 cm depth. Adult pinyon pines in Nevada had higher mortality risk when they were taller and lower mortality risk on sites with a high percentage of silt at 100-200 cm soil depths. Lastly, higher mortality risk was observed when adult pinyon pines were larger in diameter and lower mortality risk on sites with higher cool season P in Arizona. I reject my third hypothesis that pinyon pine sapling background mortality rates would be higher than their adult counterparts. Pinyon pine sapling mortality rate was highest in Colorado (2.4%), followed by Arizona (0.8%) and Nevada (0.4%). Pinyon pine saplings in this study appear to be within normal ranges of background mortality, and could reveal the potential for age-related differences in background mortality. The number of living and dead saplings was relatively low overall, which prevented use of the Cox PH model to investigate mortality factors.

The FIA dataset captured a majority of *P. monophylla* range and a large portion of *P. edulis*, and the model shows that it is an effective tool for predicting background mortality risk in pinyon pine adults across climate and environmental gradients. The significant relationships found in this study are in agreement with much of the literature regarding pinyon pine mortality (Meddens et al., 2015; Hartsell et al., 2020), despite stand characteristic data being limited. The addition of variables such as stand density would be beneficial to future analyses due to its critical role in pinyon pine mortality (Greenwood and Weisburg, 2008; Romme et al., 2009) – particularly at the individual level (Flake and Weisburg, 2019). The individual modeling approach to tree mortality used here detected potential relationships in stand-scale factors beyond the scope of this study, such as changes in climate, stand density, and likelihood of insect attack, and succeeded in identifying fine-scale influences of tree size, soil properties, and weather. This is an exciting finding considering that regional scale datasets are often unable to account for site-level variation (Peltier and Ogle, 2023). The mechanisms identified here and what is often found when studying background mortality requires an elevated understanding of how tree death occurs, which is not always a clear, direct relationship between environmental factors. Additionally, the FIA dataset successfully captured pinyon pine adult mortality events in the absence of a major disturbance or die-off event, which is useful for tracking year-to-year changes in forest structure and composition. Despite the lack of sufficient observations for saplings, it is useful to document sapling mortality to provide a point of reference for future studies. The utility of this model ranges from stand- to regional level, and the approach is simplistic enough to be used as an effective tool in forest management. The ability to describe pinyon pine mortality at a large regional scale in response to stand- and tree-scale factors is valuable to future research and in the development of adaptive management strategies (Meddens et al., 2015; Redmond et al., 2023). Forest management aimed at restoring drought-adapted species, even to intermediate levels of productivity, could buffer against expected climate change (O'Connor et al., 2017). Tree mortality is largely dependent on the degree of disturbance, conditions prior to disturbance, and site attributes (Williams et al., 2018; Zeng et al., 2020). Trees are complex, long-lived organisms, and long-term and fine-scale monitoring of tree populations is required (Peltier et al., 2017) to investigate the processes affecting background tree mortality – which is less dynamic and occurs at slower rate (Furniss et al., 2020) than disturbance-induced mortality.

CHAPTER 4

CONCLUSION

In chapter 2, I measured the hydraulic vulnerability of juvenile (∼20-30 years old) ponderosa pines growing in 6 climatically-varying locations of the SWUS and evaluated how seasonal climate, environmental conditions, and tree growth (height and diameter) were associated with differences in vulnerability. I found that juvenile and adult (> 50 years old) ponderosa pines had significant differences in p50, suggesting that hydraulic vulnerability varies between stages of tree development. Juvenile ponderosa pines in southern Nevada had more negative p50 values than juveniles in southern Colorado, southern New Mexico, and central Arizona. Compared to all other SWUS locations, southern Nevada also had significantly more severe warm season (April-September) meteorological moisture deficit, lower cool season (October-March) and warm season ψ_p, and lower soil water holding capacity. Thus, lower soil ψ_p, imparted by low warm season precipitation and physical soil characteristics, was associated with higher stress tolerance found in juvenile ponderosa pines growing in southern Nevada. I also found that vulnerability to embolism increases with height in juveniles, an association previously limited to adult trees. While my findings appear to be geographically limited to southern Nevada, these results could provide valuable insight into the future of SWUS ponderosa pine forests under warmer and drier climate conditions. Site quality, specifically soil properties, will play a major role in mediating how climate change impacts stress tolerance of ponderosa pines across the region. Despite associations between climate and environmental characteristics, the reason for higher stress tolerance in southern Nevada juveniles is unclear. 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.

In chapter 3, I used the Cox Proportional Hazards model to predict background mortality risk to several biotic and abiotic factors for adult pinyon pines in Colorado, Nevada, and Arizona over a 10-year period. I investigated the role of seasonal meteorological variables such as warm and cool season precipitation and air temperature. I also analyzed several soil and edaphic properties such as texture (% sand, silt and clay) and composition (% organic matter), and soil pH ranging 0-200 cm soil depth. Adult pinyon pines in Arizona had the greatest cumulative hazard and the lowest overall survival probability over a 10-year period compared to those in Colorado and Nevada. The leading disturbance across sites was insect attack. In support of my first hypothesis, background mortality was lower at *P. monophylla*-dominated locations compared to those occupied primarily by *P. edulis*. In partial support of my second hypothesis, greater warm season precipitation significantly decreased mortality risk for *P. edulis* in Colorado, but not for trees in Arizona. Additionally, precipitation was not the most influential factor governing background mortality for *P. edulis* in Colorado. While we expected a relationship between cool season precipitation and mortality for *P. monophylla* in Nevada, this association was only identified for *P. edulis* in Arizona. For adult pinyon pines in Colorado, greater mortality risk was observed on sites with higher cool season daily T_a max and soil pH at 30-100 cm depth, and lower mortality risk on sites with greater warm season P and higher percentage of soil organic matter at 30-100 cm depth. Adult pinyon pines in Nevada had higher mortality risk when they were taller and lower mortality risk on sites with a high percentage of silt at 100-200 cm soil depths. Lastly, higher mortality risk was observed when adult pinyon pines were larger in diameter and lower mortality risk on sites with higher cool season precipitation in Arizona. I reject my third hypothesis that pinyon pine sapling background mortality rates would be higher than their adult counterparts. Pinyon pine sapling mortality rate was highest in Colorado (2.4%), followed by Arizona (0.8%) and Nevada (0.4%). Pinyon pine saplings in this study fall within normal ranges of background mortality, and could reveal the potential for age-related differences in background mortality. The number of living and dead saplings was relatively low overall, which prevented use of the Cox PH model to investigate mortality factors. Tree mortality is largely dependent on the degree of disturbance, conditions prior to disturbance, and site attributes (Williams et al., 2018; Zeng et al., 2020). Trees are complex, long-lived organisms, and long-term and fine-scale monitoring of tree populations is required (Peltier et al., 2017) to investigate the processes affecting background tree mortality – which is less dynamic and occurs at slower rate (Furniss et al., 2020) than disturbance-induced mortality.

Together, these projects show that local variation in seasonal climate and environmental conditions can largely explain physiologic variation (e.g. stress tolerance, mortality) in western conifers. It is clear that the factors driving these processes differ between and within tree species, yet there is still uncertainty in predicting and generalizing these patterns across different environments. To add further difficulty, climate forecasts indicate that conditions will become more variable and extreme over time. Forest management aimed at restoring drought-adapted species, even to intermediate levels of productivity, could buffer against expected climate change (O'Connor et al., 2017) and maintain ideal levels of biodiversity. My results support the notion that stress tolerance and mortality are influenced by tree size/age, and the potential for juvenile and adult trees to respond differently under the similar climate and environmental conditions is a topic that requires further investigation. These findings reinforce the need for studies that investigate historic and localized patterns of tree mortality which will improve our ability to detect climate change impacts moving forward. Forest vulnerability to novel climate conditions and disturbance may depend on how species and individuals can withstand stress, and those with greater plasticity have a better chance to regenerate and persist in increasingly arid environments.

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Experience writing scientific publications and formally presenting
Independently conceptualized a project modeling background mortality of pinyon pine adults/saplings across the southwestern United States Completed a project analyzing the hydraulic vulnerability of juvenile ponderosa pines in the southwestern United States
Accessed, cleaned, and analyzed large online datasets (USFS Forest Inventory and Analysis, Web Soil Survey, DayMET, PRISM, Polaris, etc.) Accessed literature databases and reviewed numerous of scientific publications
Simultaneously managed data for two research projects
Organized field protocol and equipment for plating of 75 ponderosa pine seedlings in montane environment
Assisted in the construction of a meteorological monitoring station

Undergraduate Research Assistant – Louisiana Tech University
03/2022 – 05/2022

Followed precise protocol for sample collection, preparation, and documentation
Assisted in the construction of aquatic field experiments
Independently and accurately completed repetitive tasks
Communicated and worked efficiently with a diverse team of people
Identified fallen leaves of 25+ southeastern US tree species
Ensured safety, cleanliness, and organization of laboratory

TEACHING EXPERIENCE:
University of Nevada Las Vegas
BIOL 189L (Fundamentals of Life Science Lab) – Fall 2023, Spring 2024
BIOL 191L (Introduction to Organismal Biology Lab) – Summer 2023

AWARDS:
Grant - Graduate Student Professional Association Travel Sponsorship

Thesis Title: SEASONAL CLIMATE AND ENVIRONMENTAL CONDITIONS ASSOCIATED WITH PHYSIOLOGIC VARIATION OF SOUTHWESTERN UNITED STATES PINES

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Committee Member, Dr. Scott Abella, Ph.D.
Committee Member, Dr. Paul Schulte, Ph.D.
Graduate Faculty Representative, Dr. Marie Odile-Fortier, Ph.D