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Evidence of Competitive Release Following Overstory Mortality in a Semi-Arid Piñon-Juniper Woodland

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EVIDENCE OF COMPETIVE RELEASE FOLLOWING OVERSTORY MORTALITY IN A SEMI-ARID PIÑON-JUNIPER WOODLAND

by

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THESIS

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Evidence of Competitive Release Following Overstory Mortality in a Semi-Arid Piñon-Juniper Woodland

By

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B.S., Conservation Ecology, New Mexico State University, 2015

M.S., Biology, The University of New Mexico, 2023

Abstract

Extreme temperatures and severe drought events have led to widespread tree mortality worldwide. In semi-arid regions of the Southwest United States, these events pose a significant threat to piñon-juniper (PJ) woodlands. We studied the effects of piñon and juniper mortality on the growth and physiology of existing saplings in PJ woodlands by analyzing water status, photosynthetic activity, and tissue chemistry to gain insights into these impacts. Juniper saplings exhibited improved water status and water use efficiency in response to overstory mortality, whereas piñon saplings did not. Additionally, both piñon and juniper saplings exhibited increased photosynthetic rates, increased photosynthetic capacity, and enhanced growth rates. Our results suggest that saplings of both species responded similarly regardless of whether a mature piñon or juniper died. However, piñon saplings appeared to be more vulnerable to overstory mortality, likely due to the difference in hydraulic strategies between piñon and juniper This study enhances our understanding of the post-mortality recovery process in piñon-juniper ecosystems, providing valuable insights into the contrasting effects of piñon vs. juniper mortality as well as the distinct physiological responses exhibited by piñon and juniper saplings.

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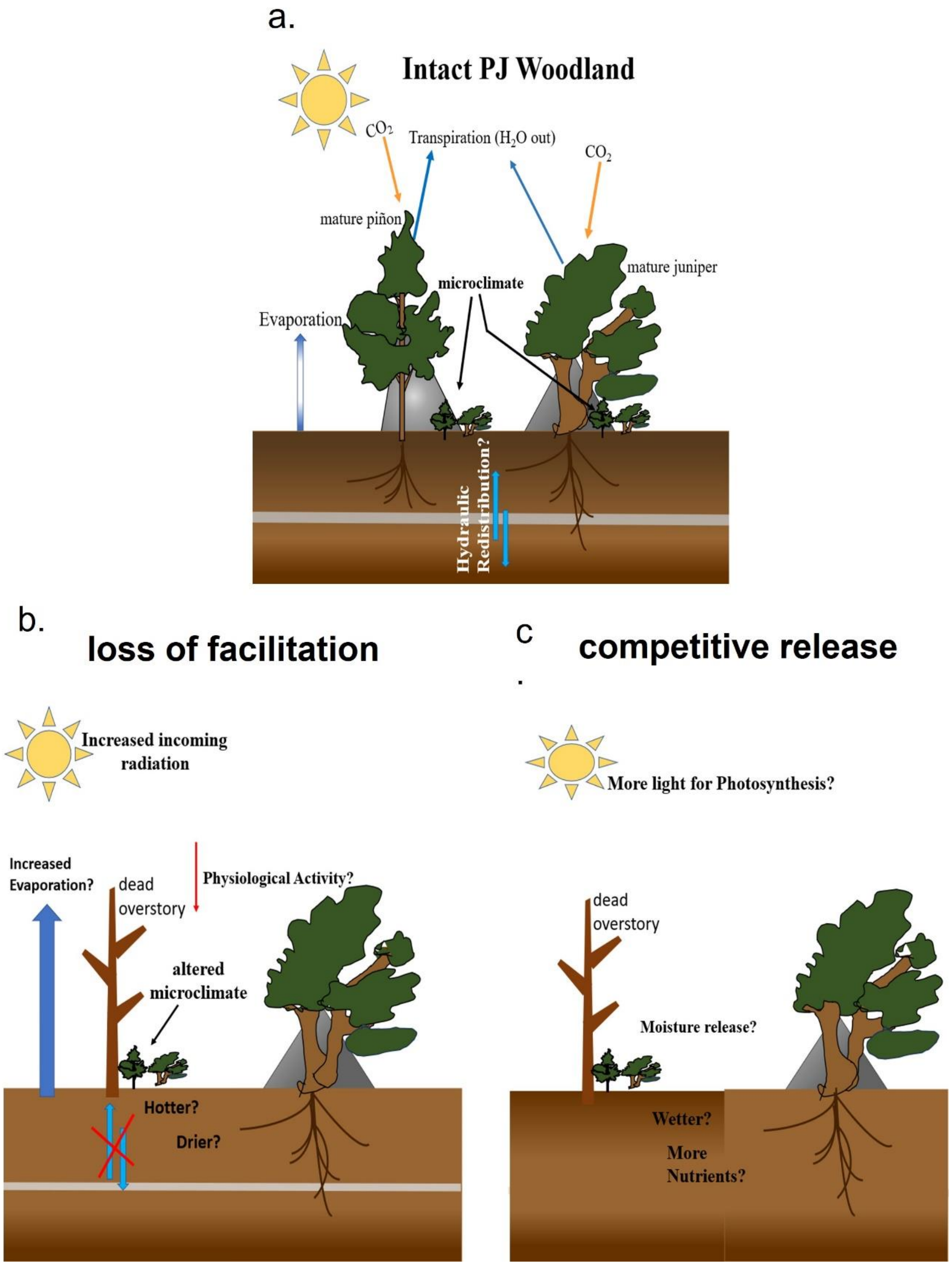
Introduction

Increased frequency of extreme temperature and severe drought in the last two decades are correlated with large-scale tree mortality events worldwide (Allen et al., 2010; Allen & Breshears, 1998). In the semi-arid Southwest U.S, extensive tree die-off events coupled to drought with unusually high temperatures are a growing concern for the sustainability of forest and woodland ecosystems in the region (Allen et al., 2010; Allen & Breshears, 1998; Marsh et al., 2022; Redmond et al., 2015, 2018). Piñon-juniper (PJ) woodlands cover an estimated 40 million ha across the western United States (Romme et al., 2009), and have been particularly sensitive to these climatic changes with mortality documented across 1.2 million ha of these woodlands (Breshears et al., 2005). Coniferous mortality events are predicted to increase throughout the Southwest (Allen et al., 2010; McDowell et al., 2011; Overpeck & Udall, 2010), potentially converting these woodlands toward shrublands or juniper savanna biomes (Allen et al., 2010; Breshears et al., 2005; Reyer et al., 2015). The recovery of piñon and juniper following mortality events will strongly influence whether these biomes will remain PJ woodlands or transition to new communities (Martínez-Vilalta & Lloret, 2016; Redmond et al., 2018). However, our ability to predict recovery of these biomes after widespread mortality is limited by insufficient information about how mortality events alter seed germination, seedling establishment, and the physiology and fate of existing saplings. In this study, we focus on the physiological response of existing saplings following overstory mortality.

Tree mortality can trigger both positive and negative impacts on sapling recruitment and recovery. In semi-arid ecosystems mature plants dominate resources, but also serve as “nurse plants", where surface radiation is reduced, soil temperature is lower, soil moisture is higher, and may be replenished via hydraulic redistribution (Fig. 1a) (Breshears et al., 1998;

Redmond et al., 2015, 2018; Royer et al., 2011; Baker, 1996; Krause, 1988). In both mesic and semi-arid biomes, overstory mortality can positively enhance sapling growth through the “release” of resources no longer being used by dead trees (Bearup et al., 2014; Dore et al., 2012; He et al., 2013; Mikkelson et al., 2013; Amiro et al. 2010; Griffin et al., 2011; Norton et al., 2015). This includes increased surface solar radiation, which can increase maximum photosynthetic rates for understory species (Fig 1c) (Griffin et al., 2004; Valladares et al., 2002). However, overstory mortality also reduces the availability of nurse plants, which can negatively impact the remaining saplings and mature trees due to increased site aridification (Fig 1b) (Duman et al., 2021, Redmond et al., 2015, 2018; Royer et al., 2011, 2012; Villegas et al., 2010; Morillas et al. 2017; Huang et al. 2021; Duniway et al., 2010; Ryel et al., 2008; Pirtel et al, 2021). Pinpointing the mechanisms that determine whether overstory mortality has positive or negative effects is crucial to predicting trajectories of recovery in this biome.

Figure 1. Conceptual figure examining the potential positive and negative consequences of overstory tree mortality on an intact PJ woodland (1a). From the perspective of loss of facilitation by nurse plants (1b) competitive release (1c).



In this study, we examined the physiological responses of *Pinus edulis* (piñon) and *Juniperus monosperma* (juniper) saplings after experimentally manipulating the mortality of mature overstory individuals of each dominant species. Our aim was to better understand the growth response and long-term physiological stability of piñon and juniper saplings following overstory mortality in PJ woodlands and if the impacts were predominantly positive or negative. Our overall questions were i) What is the physiological response of piñon and juniper saplings to the loss of overstory trees, and are the responses different between the two species? ii) do saplings of both species respond differently to piñon versus juniper mortality (either due to structural, physiological, or conspecific factors)?

Mature piñon and juniper trees differ in structure and physiology, both of which may play a role in determining the balance between positive and negative effects of overstory mortality on sapling physiology. For example, the contrasting hydraulic strategies of piñon and juniper have been attributed to observations of differential mortality of adults during drought (Adams et al., 2017; McDowell et al., 2008) and can potentially impact both how the loss of overstory species affects saplings and the physiological responses of saplings to the post-mortality moisture regime. Piñon is more isohydric, where stomata regulate transpiration to maintain leaf water potential above -2.2 megapascals (MPa), leading to stomatal closure and cessation of photosynthesis when soil water potential reaches that threshold (McDowell et al., 2008; West et al., 2008). Juniper generally exhibits an anisohydric strategy, allowing transpiration and gas exchange at low rates during at more negative soil water potentials than piñon (McDowell et al., 2008; West et al., 2008). Juniper is regarded as more drought tolerant overall due to distribution into lower elevations and drier environments (Lajtha & Getz, 1993; Romme et al., 2009). These hydraulic differences have been observed in piñon and juniper saplings (Anderegg & Anderegg, 2013) and are important to consider in understanding how the loss of overstory affects each sapling species differently. We predicted that piñon saplings may thrive with increased resources following overstory mortality, while juniper saplings may fare better in water-limited conditions.

The differences in stomatal regulation of mature trees discussed above, combined with other differences between piñon and juniper, make it challenging to predict the impact of mortality of mature piñon or juniper on saplings of each species. For example, in the absence of water limitation, adult piñon photosynthesizes and transpires at higher rates than adult juniper (Lajtha & Getz, 1993). Higher photosynthetic rates suggest piñon mortality may result in a greater competitive release of soil moisture and facilitate understory saplings. However, because piñon also has higher canopy-leaf area index (LAI) (Schuler & Smith, 1988), piñon mortality will also likely result in a larger increase in surface radiation and thus, have negative effects on soil temperature and soil water availability. Mature junipers, on the other hand, have deeper root distribution than adult piñon (Schwinning et al 2020), which might better facilitate the uptake of deep water (if present) and the redistribution of water from wetter to drier areas of the soil. Consequently, we expect the mortality of junipers to reduce the supply of water to shallow soil areas utilized by saplings during periods of water stress. We also cannot ignore that conspecific overstory mortality may reduce competition for the saplings of the next generation to thrive (Bonanomi et al., 2010; Miriti, 2006).

Materials and Methods

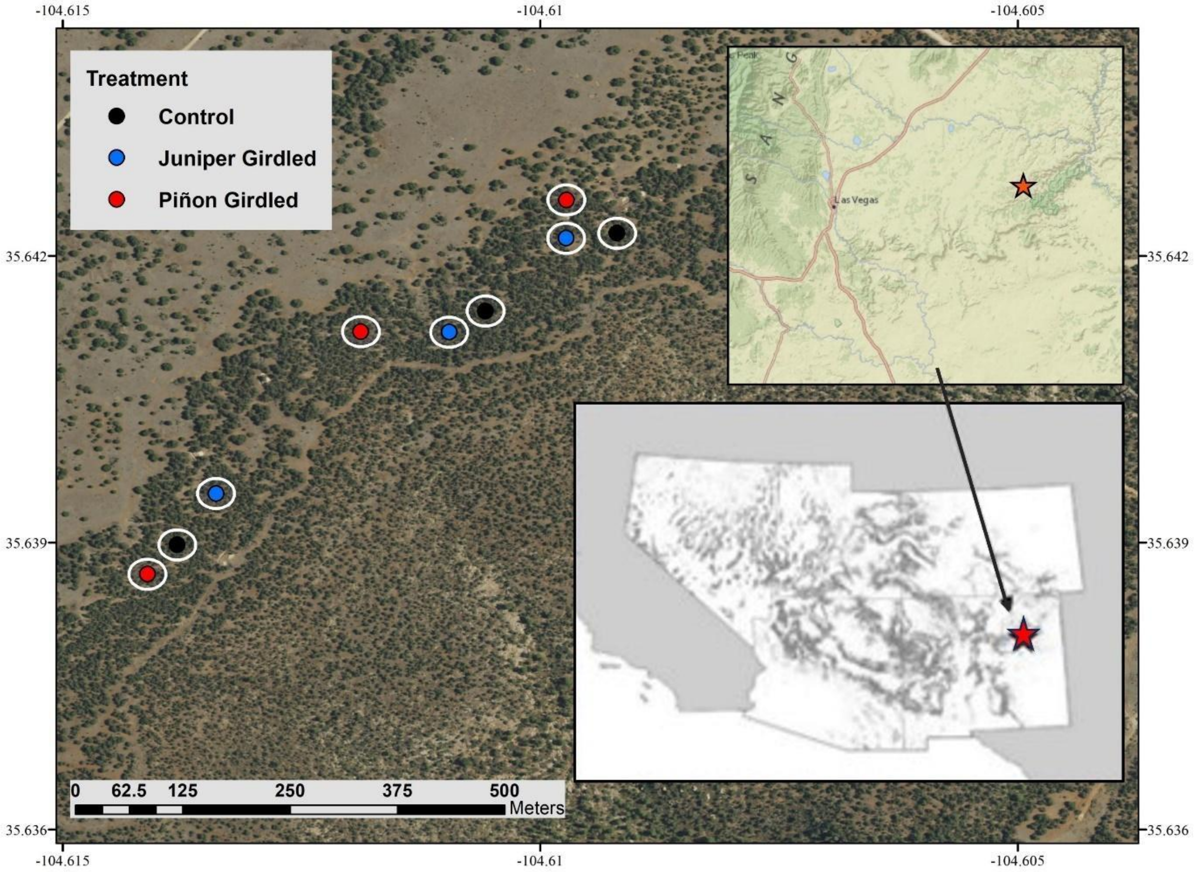
Site Description and Experimental Design

Our study site is a private ranch about 56 km east of Las Vegas, NM, (~Lat. 35.612, Long. -104.681, elevation 1927 m). Mean annual precipitation in the region is 422 mm, most of which falls between May and October and the mean annual temperature is 10.8 °C (30 year means from PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created 23 Aug 2022; Dataset: Norm91). This site is characterized as a southern Rocky Mountain piñon-juniper woodland, with dominant tree species of piñon pine (*Pinus edulis,* Engelm.) and one-seed juniper [*Juniperus monosperma* (Engelm.) Sarg.]. In general, soils are relatively shallow and characterized by clay loams with organic accumulations at the surface from 15-35 cm, which transition to gravelly partially cemented calcium carbonate caliche layers, and then hard caliche layers between 40-90 cm depth (Schwinning et al., 2020).

We used girdling to trigger piñon and juniper mortality. The experimental design included nine 1000 m2 plots arranged in three blocks, with three plots in each block randomly selected as a control, one as a piñon girdle plot and the other as a juniper girdle plot (Fig. 2). In the treatment plots, all piñon or juniper trees above a diameter of > 3 cm at breast height were girdled in October 2017 using a chainsaw, to disrupt the transport of photoassimilates in the phloem by cutting through the phloem into the cambium of stem around the entire circumference of the tree (Morillas et al., 2017). We used sap flow probes installed in the trees prior to girdling to track the decline in transpiration rates in the girdled trees and determine when the trees were no longer functioning, which occurred in Feb 2018 for juniper, and April 2018 for piñon across the plots.

The sapling physiological measurements reported here were made from September 2018 through May 2020. In each girdled plot we selected and tagged five piñon and five juniper saplings, defined as juveniles between 30-130 cm in height, under the canopy of dead trees. In the control plots, we tagged five saplings of each species under live piñon and live juniper overstory trees. We used this same set of saplings for all the leaf water potential measurements taken throughout the study. However, for the light response curves and tissue chemistry measurements we took a subset of three from the original five saplings selected under each treatment type.

Figure 2. Overview of study area illustrating the layout of the treatment plots and blocked design across the landscape. Including the general location of our research site at Hobo Ranch in northern New Mexico and the distribution of piñon-juniper woodlands across the semi-arid southwest. This map was created using ESRI software (ArcMap version 10.8.1).



Soil Water Potential

To evaluate the effect of tree mortality on soil water availability, we used soil psychrometers (PST-55, Wescor, Logan, UT, USA) installed in the soil at depths of 15, 30, and 60 cm across treatments six months prior to girdling. Probes were installed in six pits per plot with four pits located between canopy clusters and two pits under the canopy trees. Because piñon and juniper canopies and roots are often intermingled, we did not distinguish between under piñon or under juniper for the canopy soil pits. All psychrometers were measured once every 15 minutes using a datalogger (Campbell Scientific, model CR6, Logan Utah, USA). We focused on soil water potential at depths of 15 and 30 cm since piñon and juniper sapling roots typically have a rooting depth between 22-34 cm (Pirtel et al., 2021).

Physiological measurements

Leaf Water Potential

To assess changes in saplings' water status and estimate if overstory mortality of mature piñon or juniper affected water movement through the plant (pre-dawn - midday difference, or $\Delta\Psi$), we measured sapling leaf water potential (Ψ). We used Scholander pressure chambers (Model 1000, PMS Instrument Company, Albany, OR, USA) to measure pre-dawn and midday water Ψ in piñon and juniper saplings across all plots. We took these measurements on September 14, 2018 (Fall 2018), June 25, 2019 (Summer 2019), and June 2, 2020 (Summer 2020). For pre-dawn measurements we collected two twigs per sapling between 4:00am and 5:30am, placed them in a plastic bag with a moistened paper towel and stored them in a cooler until all samples were collected then took measurements on them. We collected stems for midday measurements between 12:00 pm and 2:00 pm using the same method but measured these immediately after collection. Samples were generally measured within an hour of collection at predawn and within 15 minutes of collection at midday.

Light Response Curves

We measured light response curves in fall of 2018 (Sept. 26-27) and fall of 2019 (Oct. 7-8) using a portable gas exchange system (LI-6400, Li-Cor Inc., Lincoln, NE, USA) with 2x3cm light-source chamber (6400-02B LED, Li-Cor Inc) to assess if the change in incoming radiation after mortality of piñon or juniper stimulated a change in the photosynthetic parameters of piñon or juniper saplings. In each year, we took measurements on two consecutive sunny days between the hours of 10 am and 1:30 pm. Measurements were taken at ambient temperature ranging from (20 to 30°C), ambient relative humidity ranging from (5.9 – 56.2%) and a CO_2 concentration of 400 ppm with an airflow rate set at 400 µmol s^{-1}. We clamped the light-source chamber around a small bunch of foliage on the current year's growth of a south facing twig and recorded the carbon assimilation rate (µmol m^{-2}s-1) at 10 different photon flux density (PPFD) values decreasing from 2000-0 (µmol m^{-2}s -1). We collected the foliage from inside of the chamber after the light response curves were taken on each sample and put them into a humidified plastic bag in a cooler on ice and transported them back to the lab where color scans of each sample were made on a flatbed scanner. We calculated the projected leaf area of each sample (usually between 3.5 -12 cm^2) using ImageJ software (Rasband, 2018) and used that value to normalize the light response curve data. To account for the cylindrical shape of juniper foliage we calculated the actual leaf area by multiplying the projected leaf area by 3.23 (Cregg, 1992). We used the fit_aq_curve function in the R-package *photosynthesis* (Stinziano et al., 2021; R Core Team, 2020), which employs the Marshall et al. (1980) non-rectangular hyperbola model to calculate the following photosynthetic parameters: light saturated rate of photosynthesis (A_{max}, µmol m-2 s-1), light compensation point (LCP), rate of dark respiration (Rd, m^{-2} s^{-1}) and quantum yield (Φ).

Tissue Chemistry

To assess the effect of overstory mortality on sapling intrinsic water use efficiency, carbon and nitrogen cycling, photosynthetic capacity, and nutrient availability, we determined carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios and the C:N ratio in leaf material from piñon and juniper saplings. We collected samples from the current year's growth on fully developed foliage on October 8, 2019. We stored the collected materials on ice in a dark cooler and transported them back to the lab where we freeze-dried (FreeZone 4.5Plus, LabConCo, Kansas City, MO) and ground them using liquid nitrogen and a mortar and pestle and then stored them in a 1.5 ml centrifuge tube (sample weight ranging from 1.8-3.8 mg). We transported these samples to University of New Mexico Center for Stable Isotopes, where they were analyzed using a mass spectrometer (Delta Plus; Thermo Fisher Inc., Waltham, MA, USA) connected to an elemental analyzer (ECS 4010; Costech Analytical Technologies, Valencia, CA, USA). Carbon isotope ratios of the samples were expressed as deviations per mil (‰) from the Vienna PeeDee Belmnite international standard and calculated as follows:

$$\delta^{13}C = [(R_{sample} - R_{standard})/ R_{standard}] \times 1000‰, \qquad \text{eq. 1}$$

where R is the molar ratio $^{13}C/^{12}C$ of the sample or PeeDee standard. Nitrogen stable isotope ratios were calculated the same way, where R is the molar ratio of $^{15}N/^{14}N$ and expressed as deviations per mil from the atmospheric nitrogen standard (Coplen, 2011).

Leaf Chlorophyll Content

We collected south-facing foliage from piñon and juniper saplings on May 22, 2019 (from 2018 growing season) and October 8, 2019 (from 2019 growing season) for chlorophyll content analysis to evaluate whether overstory mortality of piñon or juniper triggered a change in chlorophyll. We stored collected materials on ice in a dark cooler for transport to the lab, where we freeze-dried them (FreeZone 4.5Plus, LabConCo, Kansas City, MO) for 24 hours. Once dried, we used razor blades to chop up subsamples into 1-2 mm long pieces and weighed them into vials containing 10 ml of 80% acetone solution. Sample weights ranged from 0.05-0.149 g (90% of them were within the 0.8-0.1g range). We allowed 48 hours extraction time in a dark fridge (to prevent degradation), by which time plant materials had turned completely white (Eitel et al., 2011; Mackinney, 1941). We analyzed the chlorophyll/acetone solutions two times each with a spectrophotometer (50 Bio UV-Vis, Varian Cary, Palo Alto, CA) with absorbance filters set to read at 646.6 nm and 663.6 nm (Porra, 2005; Porra et al., 1989). We calculated chlorophyll a, b, and total chlorophyll (a + b) using the following equations and then converted the result to mg/g for analysis (Porra, 2005; Porra et al., 1989).

Chl a	$[\text{Chl } a] = 12.25\ E663.6 - 2.55\ E646.6$	$(([\text{Chl } a]\ ^{*}10\text{ml})/\text{sample weight in grams})$
Chl b	$[\text{Chl } b] = 20.31\ E646.6 - 4.91\ E663.6$	$(([\text{Chl b}]\ ^{*}10\text{ml})/\text{sample weight in grams})$
Chl a+b	$[\text{Chl } a + b] = 17.76\ E646.6 + 7.34\ E663.6$	$(([\text{Chl } a + b]\ ^{*}10\text{ml})/\text{sample weight in grams})$

Statistical Analysis

We used RStudio statistical software (Version 4.2.2; RStudio Team 2020) for all analyses. We constructed multilevel linear mixed-effects models (*lme*) using the "lme4" package to analyze each response variable. The models included fixed effects of Overstory Status (OvStatus: live or dead), Overstory Species (OvSp: piñon or juniper), Sapling Species (SapSp: piñon or juniper), measurement period (year) when applicable, their interactions, and the random effects of plot nested in block (~1|Block/plot).

We examined the relationship between pre-dawn water Ψ and the difference between pre-dawn and midday (ΔΨ) to assess the rate of transpiration vs soil water availability. We employed a linear mixed-effects regression model (*lmer*) to investigate the general relationship (all measurement periods) between pre-dawn water Ψ and ΔΨ in response to overstory mortality. Our fixed effects included pre-dawn Ψ, OvStatus, OvSpecies, and their interactions. Due to a significant interaction between pre-dawn Ψ and sapling species (SapSp), we analyzed piñon and juniper saplings separately. To account for random variation of the measurement period (year), we added year as a random intercept (year|Block/plot) in our models.

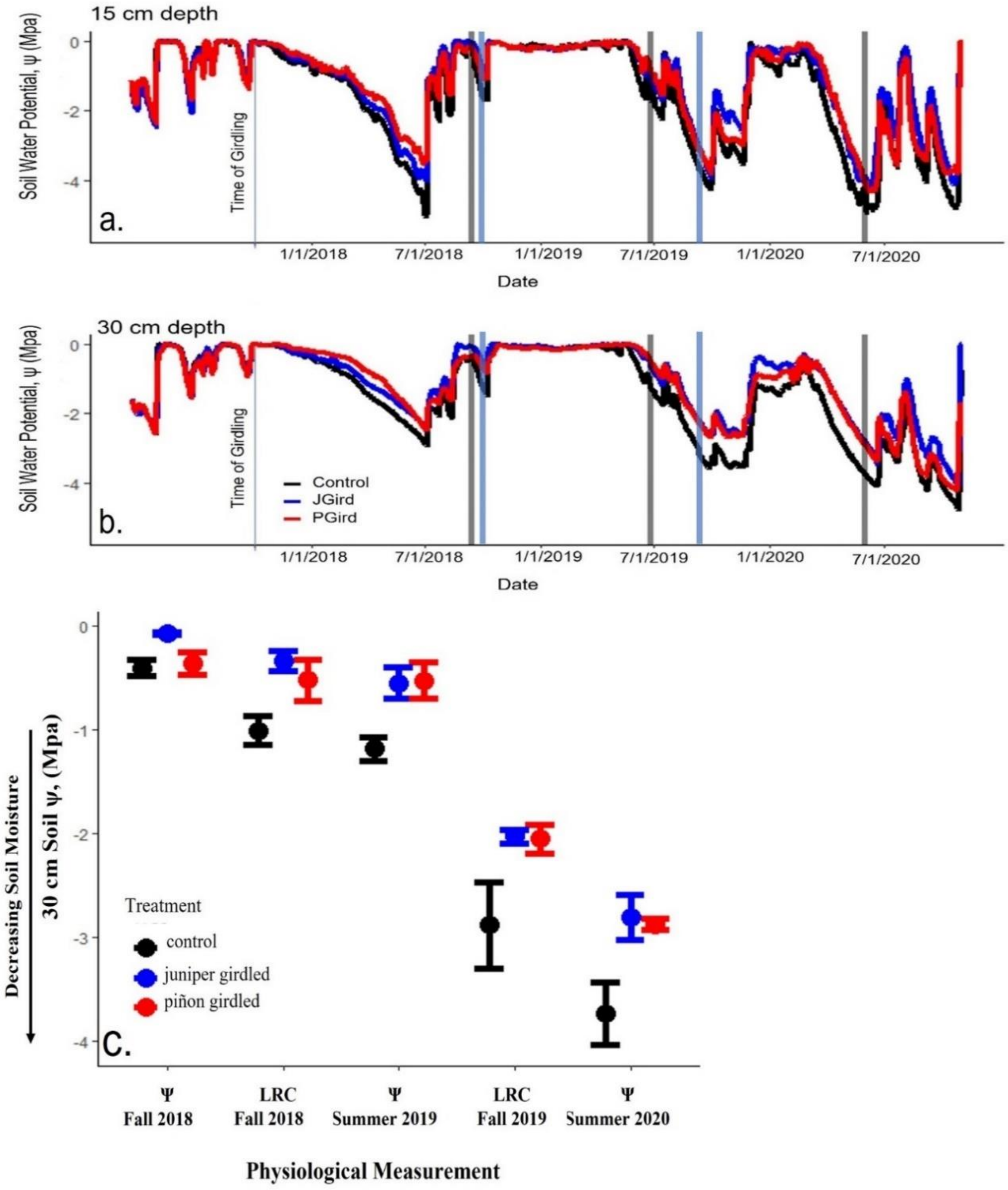
We ran an ANOVA from the R package “car” on each model, considering p-values < 0.05 as statistically significant for main effects and their interactions. Replication was achieved at the block-level with n = 3 since individual measurements were averaged within plots. Assumptions of normality of residuals were evaluated and confirmed using the Shapiro-Wilk test, and homoscedasticity was checked by plotting the residuals vs. predicted values for each model. All figures were generated using the R package “ggplot2”, and error bars represent the standard errors of the means in all the point plots. Because mature piñon and juniper were girdled on different plots the 'under dead juniper' and 'under dead piñon' measurements were conducted in different plots, while the 'under live juniper' and 'under live piñon' measurements were conducted in the same (control) plots. Thus, the dead vs alive contrast implicitly compared the girdle treatment with the control.

Results

Soil Water Availability

Plots with dead trees (either piñon or juniper overstory) exhibited less negative soil water potentials at 15 and 30 cm depths, indicating greater water availability. This increased water availability under dead trees compared to live ones was most pronounced during dry down periods (Fig. 3). with the largest differences at 30 cm recorded in June 2020, the driest period (Fig. 3 c).

Figure 3. Soil water Ψ at 15 (3a) and 30 cm (3b) depths between the start of the experiment through study. Gray and blue bars indicate times when leaf water Ψ and light response curve measurements were taken. Figure 3c, shows the mean soil water Ψ values when these measurements were taken.



Sapling Water Status

In the summer of 2019 and 2020, juniper saplings under dead trees exhibited higher pre-dawn ψ (less negative) compared to those under live trees. This difference was most noticeable in the drier summer of 2020 (Fig. 4, Table 1: OvStatus - $p < 0.001$, OvStatus*year - $p < 0.001$). The increase in pre-dawn ψ observed in juniper saplings under dead trees did not depend on whether the overstory dead tree was piñon or juniper. However, we did not observe the same response in piñon saplings in any of the pre-dawn ψ measurements (Fig. 4, Table 1: OvStatus*SapSp - $p < 0.0001$, OvStatus*SapSp*year - $p < 0.0001$, OvStatus*SapSp*OvSp- $p = 0.0359$). Similarly, in the summer of 2020, juniper saplings had a less negative midday ψ under dead trees compared to live trees (Fig. 4, Table 1: girdled - $p < 0.0001$, OvStatus*year - $p < 0.0001$). Piñon saplings only displayed a less negative midday ψ under live piñon trees compared to dead ones in the summer of 2019 (Fig. 4), with no significant differences in other pre-dawn or midday ψ measurements (Fig. 4).

Figure 4. Mean values for pre-dawn and midday Ψ measurements in piñon (d, e, f, j, k, l) and juniper saplings (a, b, c, g, h, i) across treatments. Overstory species: juniper (purple) or piñon (maroon), overstory status: live (closed circles) or dead (open circles). Across three measurement periods: Fall 2018, Summer 2019, and Summer 2020.

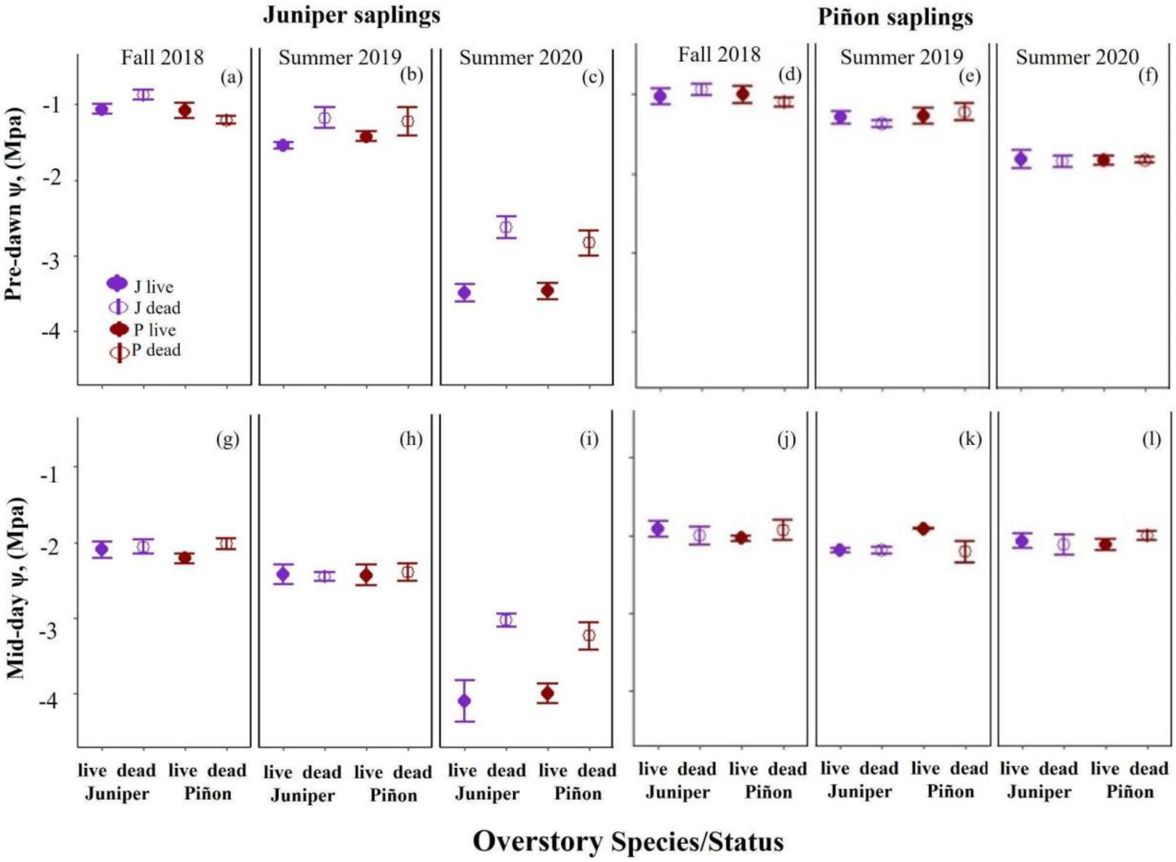


Table 1. Mean and standard errors for pre-dawn (pd) and midday (md) Ψ for piñon and juniper saplings (SapSp: piñon or juniper) organized into overstory species/status for September 2018, June 2019, and June 2020.

	Ψ (pd)			**Ψ (md)**		
	2018	2019	2020	2018	2019	2020
Piñon saplings						
juniper live	-1.03 ±0.1	-1.29±0.08	-1.82±0.11	-1.93 ±0.1	-2.19±0.02	-2.07±0.09
juniper dead	-0.94±0.07	-1.37±0.05	-1.85±0.07	-2.01±0.12	-2.19±0.04	-2.12±0.13
piñon live	-1.00±0.11	-1.27±0.10	-1.83±0.06	-2.04±0.03	-1.91±0.01	-2.13±0.08
piñon dead	-1.10±0.06	-1.23±0.11	-1.83±0.04	-1.93±0.13	-2.21±0.13	-2.01±0.06
Juniper saplings						
juniper live	-1.07±0.07	-1.55±0.04	-3.49±0.12	-2.10±0.11	-2.43±0.13	-4.10±0.27
juniper dead	-0.88±0.06	-1.18±0.14	-2.63±0.15	-2.06±0.09	-2.45±0.05	-3.03±0.08
piñon live	-1.09±0.10	-1.43±0.07	-3.47±0.11	-2.21±0.07	-2.43±0.14	-3.99±0.13
piñon dead	-1.21±0.05	-1.23±0.19	-2.83±0.17	-2.02±0.07	-2.40±0.12	-3.23±0.18

Pre-dawn ψ strongly influenced the ΔΨ of pre-dawn and midday measurements (proxy for transpiration), (Fig 5. Table 2). The overstory status (live or dead) did not impact ΔΨ in piñon saplings. However, piñon saplings ceased photosynthesis at a pre-dawn Ψ of approximately -2.2 MPa. Juniper saplings under dead trees showed significantly reduced ΔΨ with decreasing pre-dawn Ψ (Fig 5. Table 2), indicating a more conservative water use strategy during water stress. This response was most pronounced under the canopy of dead juniper vs. live juniper (Table 2).

Figure 5. Pre-dawn Ψ vs. ΔΨ across treatments. Note that the x-axis is inverted for visualization purposes. Juniper saplings (5a) had a significantly steeper slope under the canopy of dead trees (green and purple) vs. live trees (coral and blue), p-value = 0.002, and this was most pronounced under dead juniper (green) vs. live juniper (coral), p-value = 0.0233.

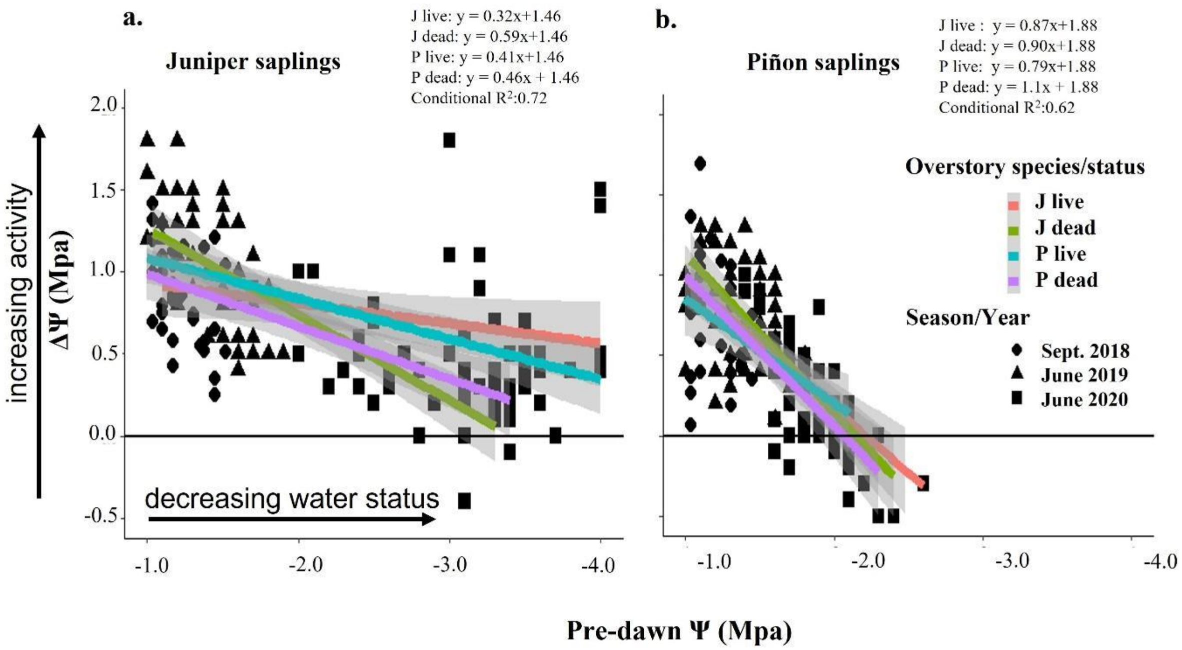


Table 2. P-values from ANOVA for fixed effects and their interaction terms are presented here for pre-dawn Ψ vs. ΔΨ analysis for piñon and juniper saplings. Piñon and juniper saplings were analyzed separately due to the significant difference we found for the interaction effect pre-dawn water potential and saplings species have on the dependent variable (ΔΨ).

Significance	**Piñon saplings**	**Juniper saplings**
pd.WP	**<0.0001**	**< 0.0001**
OvStatus	0.5062	**0.0020**
pd.WP*OvStatus	0.1834	**0.0022**
pd.WP*OvStatus*OvSpecies	0.2604	**0.0233**

Photosynthetic Activity

During both measurement periods, light saturated rate of photosynthesis (A_{max}) increased significantly in piñon and juniper saplings under the canopy of dead trees compared to live trees (Fig 6., OvStatus: $p < 0.0001$) and this response was independent of the overstory species that died. In 2018, LCP and R_d in juniper saplings were highest under dead piñon trees, and in 2019, juniper saplings LCP was highest under both dead juniper and dead piñon canopies (OvStatus: $p < 0.0001$ and $p < 0.001$). R_d in piñon saplings increased under dead piñon canopies in 2018 but did not have the same response in 2019 (OvStatus* OvSp*year: p - 0.0047, OvStatus*SapSp*year: p - 0.0487). LCP remained the same in piñon saplings across treatment types for both measurement periods. There was no change in Φ in either of the sapling species in response to overstory mortality for either of the measurement periods.

Figure 6. Mean values of light saturated rate of photosynthesis (A_{max}), increased for juniper saplings (left panel, a and b) and piñon saplings (right panel, c and d) after girdling. Note that scales differ between saplings species for visualization purposes.

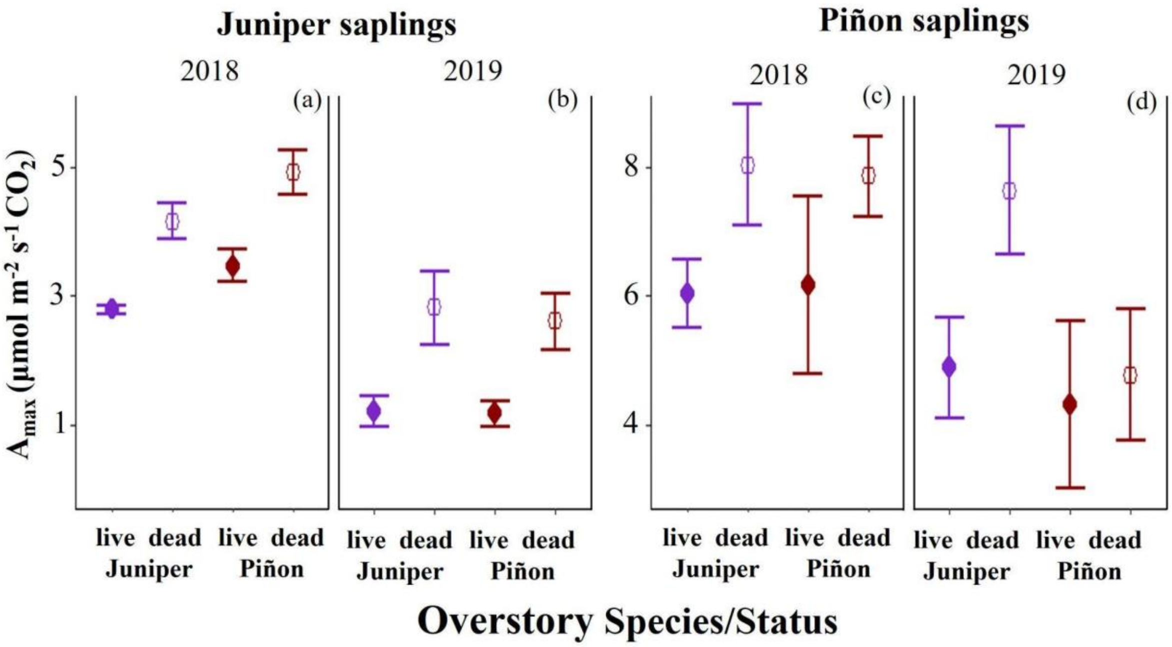


Table 3. Photosynthetic parameters from light response curves. Light saturated rate of photosynthesis: A_{max} (μmol m^{-2} s^{-1} CO_2), Light compensation point: LCP (μmol m^{-2} s^{-1} photons), Rate of dark respiration: R_d (μmol m^{-2} s^{-1} CO_2).

	A_{max}		**LCP**		R_d	
	2018	2019	2018	2019	2018	2019
Piñon saplings						
overstory species/status						
live juniper	6.04 ±0.5	4.88 ±0.8	47.8 ±11.8	22.4 ±1.8	1.05 ±0.3	0.63 ±0.1
dead juniper	8.03 ±0.9	7.63 ±1.0	42.8 ±19.4	36.7 ±5.9	0.86 ±0.4	1.25 ±0.3
live piñon	6.16 ±1.4	4.31 ±1.3	47.6 ±18.1	30.0 ±8.3	0.94 ±0.2	0.67 ±0.1
dead piñon	7.85 ±0.6	4.77 ±1.0	52.4 ±3.6	38.7 ±12.5	1.30 ±0.2	0.85 ±0.2
Juniper Saplings						
overstory species/status						
live juniper	2.78 ±0.05	1.22 ±0.2	32.3 ±3.4	28.7 ±4.1	0.35 ±0.0	0.35 ±0.2
dead juniper	4.15 ±0.3	2.82 ±0.6	44.2 ±12.6	47.3 ±5.5	0.53 ±0.2	0.56 ±0.2
live piñon	3.46 ±0.2	1.18 ±0.2	37.7 ±10.9	32.9 ±6.9	0.45 ±0.1	0.29 ±0.1
dead piñon	4.90 ±0.3	2.60 ±0.4	85.8 ±14.3	44.9 ±1.1	0.96 ±0.1	0.56 ±0.1

Tissue Chemistry

Foliar N content

Foliar N content in juniper saplings under dead trees was significantly (30%) higher than saplings under live trees and the overstory species that died did not influence this response (Fig. 7, Table 3). Foliar N content in piñon saplings under dead trees was 12.5% higher than in saplings under live trees. Juniper and piñon saplings C:N ratio were 28% and 17% lower, respectively, under dead trees, compared to live trees (Fig 7, Table 4), either indicating an enhanced growth rate or increased nitrogen availability. There was no change in foliar C content in response to overstory mortality for piñon or juniper saplings (Table 4).

Carbon and Nitrogen Isotopes

Juniper sapling $\delta^{13}C$ under dead trees was significantly higher (less negative) than under live trees, and this difference did not depend on whether the dead overstory tree was piñon or juniper (Fig 7, Table 3). Piñon saplings $\delta^{13}C$ values remained unchanged after overstory mortality (Fig 7, Table 4). Juniper saplings had a 44% more enriched δ15N under dead trees vs. live trees and this did not depend on the overstory species that died (Fig 7, Table 4). We recorded 126% more enriched δ15N in piñon saplings under dead piñon trees only, but δ15N remained unchanged in piñon saplings growing under dead juniper (Fig 7, Table 4).

Figure 7. Mean values for carbon isotope ratio: δ13C (°/₀₀), nitrogen isotope ratio: δ15N (°/₀₀), percent foliar N, and foliar C:N ratio by dry weight of piñon (right panel) and juniper saplings (left panel).

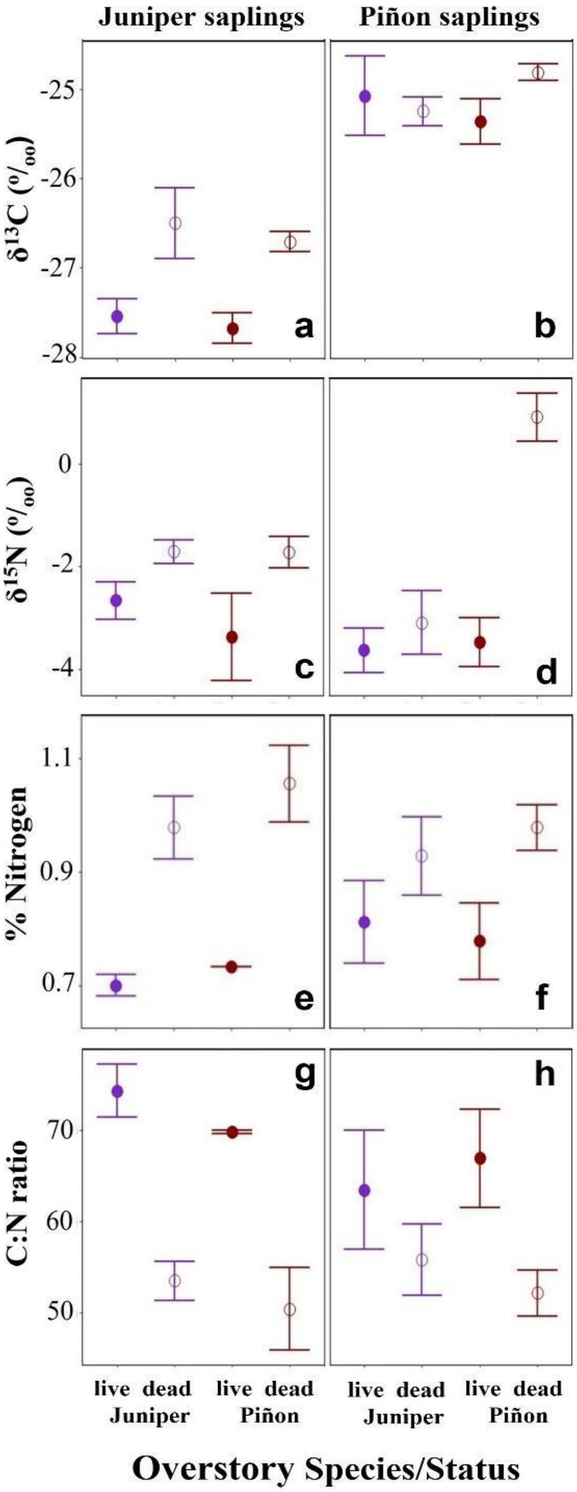


Table 4. Mean and standard errors for carbon isotope ratio: δ13C ($^{o}/_{oo}$), nitrogen isotope ratio: δ15N ($^{o}/_{oo}$), percent foliar N percent foliar C, and foliar C:N ratio by dry weight of piñon and juniper saplings across treatments. P-values from ANOVA results presented here.

	δ13C	δ15N	% Foliar N	% Foliar C	C:N ratio
Piñon saplings					
live juniper	-25.1±0.4	-3.6±0.4	0.8±0.1	50.0±0.04	63.5±6.5
dead juniper	-25.3±0.2	-3.1±0.6	0.9±0.1	50.5±0.5	55.9±3.9
live piñon	-25.4±0.3	-3.5±0.5	0.8±0.1	50.6±0.3	66.9±5.4
dead piñon	-24.8±0.1	0.92±0.5	0.9±0.0	50.3±0.4	52.2±2.5
Juniper Saplings					
live juniper	-27.5±0.2	-2.7±0.4	0.7±0.2	51.2±0.01	74.3±2.9
dead juniper	-26.5±0.4	-1.7±0.2	1.0±0.	51.0±0.5	53.5±2.8
live piñon	-27.7±0.2	-3.4±0.9	0.7±0.0	51.0±0.1	69.9±0.2
dead piñon	-26.7±0.1	-1.7±0.3	1.1±0.01	51.0±0.4	50.4±4.5
Significance					
OvStatus	**0.0020**	**< 0.0001**	**< 0.0001**	0.9515	**< 0.0001**
OvStatus*OvSp	0.4041	**< 0.0001**	0.4235	0.5672	0.6180
OvStatus*SapSp	**0.0281**	**0.0125**	**0.0314**	0.5968	**0.0410**
OvStatus*OvSp *SapSp	0.2724	**0.0020**	0.8495	0.3904	0.3779

Chlorophyll Content

In May 2018, chlorophyll content (a+b) of juniper saplings was significantly higher under dead juniper vs. live juniper, and piñon saplings had higher chlorophyll content (a+b) under dead piñon vs. live piñon (Fig 8, OvStatus*OvSp: p - 0.0234, OvStatus*OvSp* SapSp: p - 0.0067). We did not observe a difference in chlorophyll content in October 2019 in either of the sapling species under the canopy of dead trees vs. live trees. The ratio of chlorophyll a:b was similar across treatments for both measurement periods in both piñon and juniper saplings.

Figure 8. Mean values for total chlorophyll content: chlorophyll (a+b) for piñon (c, d) and juniper saplings (a, b) and chlorophyll a:b ratio (piñon: g, h and juniper: e, f) from May 2019 (2018 growing season) and October 2019 (2019 growing season) in piñon and juniper saplings across treatments.

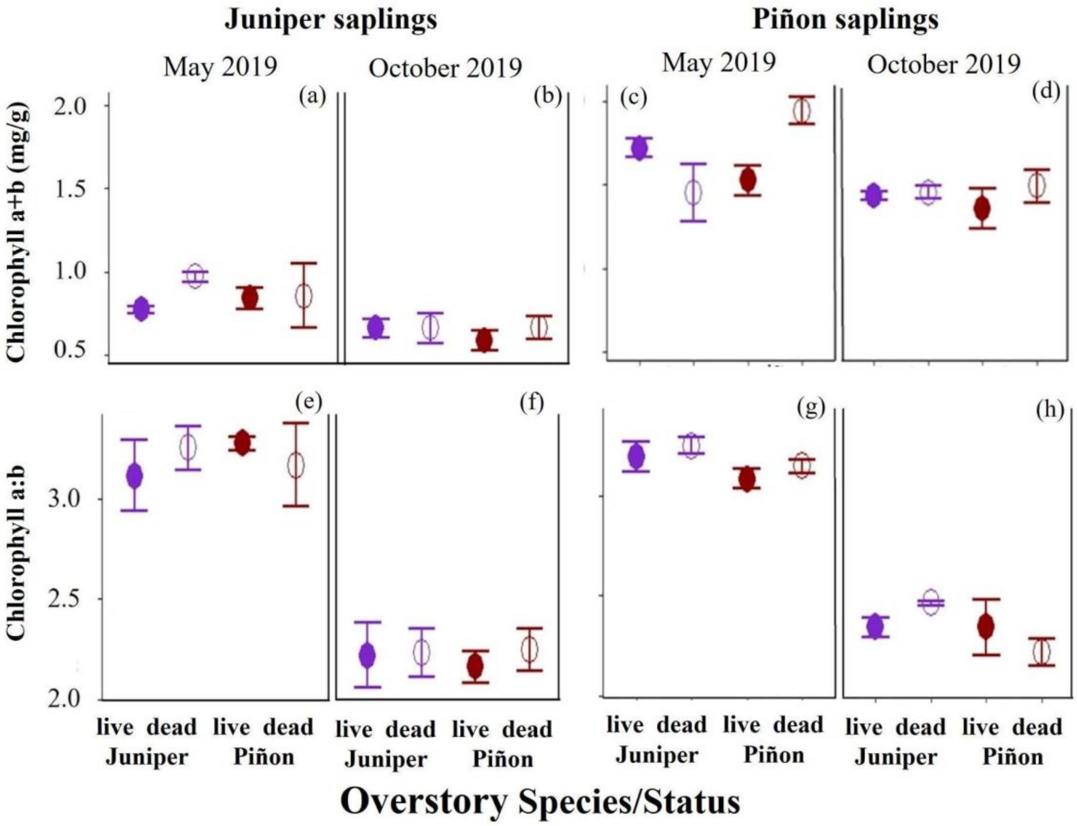


Table 5. Means and standard errors for chlorophyll a + b for piñon and juniper saplings across treatment types.

	Chl a + b (mg/g)	
	2018	2019
Juniper Saplings		
live juniper	0.77 ± 0.02	0.68 ± 0.07
dead juniper	0.97 ± 0.03	0.66 ± 0.09
live piñon	0.84 ± 0.06	0.59 ± 0.06
dead piñon	0.86 ± 0.19	0.66 ± 0.07
Piñon Saplings		
live juniper	1.72 ± 0.06	1.43 ± 0.02
dead juniper	1.45 ± 0.17	1.40 ± 0.01
live piñon	1.52 ± 0.09	1.35 ± 0.12
dead piñon	1.94 ± 0.08	1.49 ± 0.10

Discussion

Piñon-juniper woodlands face potential biome level shifts following large-scale die-off events associated with earth’s changing climate (Allen et al., 2010; Breshears et al., 2005; Reyer et al., 2015). Biomes change when seedlings and saplings are filtered non-randomly by the disturbance to the overhead canopy, post-disturbance climate, and the interaction of two. Understanding the physiological responses of piñon and juniper saplings following mortality events is needed to predict filtering during the recruitment of the future overstory trees and the trajectory of recovery. Overwhelmingly negative responses (from reduced facilitation) do not favor swift recovery from disturbance. In contrast, primarily positive effects (from competition release) would tend to favor long-term persistence of PJ woodlands despite challenges imposed by disturbance (Fig. 1). This study addressed the overarching question of whether positive or negative responses dominate during recovery and sought to identify the physiological basis for these outcomes.

We hypothesized that piñon saplings would be more negatively affected by overstory mortality than juniper saplings because of the tendency to decrease stomatal conductance at higher soil water availability as drought progresses than juniper. Although piñon saplings in our study did not have as strong of a positive response to overstory mortality as juniper saplings in as many physiological parameters (Figs 4, 5, 6 and 7, Tables 2 and 4), overall, both pinon and juniper saplings in our study were surprisingly either not affected or benefitted from overstory tree mortality. We observed very few conspecific interactions, and the sapling response did not depend on which overstory species died (Figs. 4-8). Together, this research suggests that both piñon and juniper saplings in this disturbed woodland will continue to grow, and without further disturbance or drastic change in climate, this site will likely return to an intact PJ woodland. However, there are some caveats to these results based on the climatic variation and edaphic characteristics across the distribution of the range that will be discussed in more detail later.

Short and Long-Term Beneficial Effects of Overstory Mortality

The simultaneous increase in water and light enabled saplings to benefit from improved light conditions, at least in the short-term. However, this outcome is also likely dependent upon available soil water. In the event of an extreme drought year, decreased soil water could have dictated the response to increased exposure to radiation, with adverse effects (Bansbach, 2019; Liebrecht, 2018; Morillas et al., 2017).

The positive physiological changes in piñon and juniper saplings under dead trees could also indicate shifts in their long-term physiological processes, including faster annual growth rates and increased soil nutrient availability, both of which would accelerate forest recovery. Increased foliar N and decreased C:N ratio under the canopy of dead trees vs. live trees in piñon and juniper saplings suggest that overstory mortality improved the photosynthetic capacity and growth rates in both saplings species (Ellsworth & Reich, 1992; Field, 1986; Livingston et al., 1998; Zhang et al., 2020). Higher $\delta^{13}C$ in juniper saplings under dead trees indicates enhanced water use efficiency, likely due to increased carboxylation capacity (Farquhar et al., 1989), and aligns with the pre-dawn water Ψ vs. $\Delta\Psi$ results (Fig. 5, Table 2), where juniper saplings exhibited a faster decrease in $\Delta\Psi$ under dead trees compared to live trees. These outcomes suggest a potential shift towards a more conservative physiology in terms of water use. Higher $\delta^{15}N$ of juniper saplings under dead trees suggests a shift in nitrogen source and potentially greater nutrient availability in the soil (Craine et al., 2015), possibly due to increased leaf litter from mature trees that died, supported by increased foliar N content measurements (Craine et al., 2009; Griffin et al., 2011; Norton et al., 2015).

Differential Species-Specific Responses to Overstory Mortality

Although both sapling species responded beneficially to overstory mortality, juniper saplings exhibited a much stronger response than piñon saplings. We suggest the more limited response in piñon, particularly as drought progressed in our experiment (Fig 5) can be attributed to piñon's isohydric hydraulic strategy, preventing it from exploiting favorable changes in soil water potential below approximately -2.2 MPa (McDowell et al., 2008; West et al., 2008). These findings suggest that piñon saplings, like mature piñon trees, are more vulnerable to overstory mortality in the face of a hotter and drier climate (Anderegg & Anderegg, 2013; Limousin et al., 2013; McDowell et al., 2008; West et al., 2007).

Our results did not support the general influence of a conspecific relationship between mature trees and saplings dictating the physiological response of piñon and juniper saplings to overstory mortality. However, higher $\delta^{15}N$ enrichment in piñon saplings under dead piñon (Fig. 7d, Table 4) suggests a piñon mortality may trigger a potential shift in sapling nitrogen cycling and nutrient uptake (Craine et al., 2009, 2015). This response may be facilitated by the loss of mycorrhizal (endomycorrhizal) fungi due to piñon mortality (Morte et al., 2001; Dickie et al., 2002; Haskins & Gehring, 2004) or alternatively reduced competition for nitrogen resources among conspecifics (Norton et al., 2015). Juniper saplings also exhibited a slightly stronger response in $\Delta\Psi$ versus pre-dawn Ψ under dead juniper compared to under dead piñon; and although we observed a conspecific response in both juniper and piñon saplings, as indicated by chlorophyll content in the 2018 foliage (Fig. 8a, 8c, Table: 5), the pattern was inconsistent in the 2019 foliage (Fig. 8b, 8d), These observed instances suggest conspecific mortality impacts are likely not important but may warrant further investigation for conclusive insights.

Other Factors Dictating Ecosystem Resilience in PJ Woodlands

Both piñon and juniper saplings benefited from competitive release following overstory mortality. Increased A_{max} triggered by improved access to light following canopy loss is consistent with the findings in other ecosystems that have experienced overstory mortality (Dalmolin et al., 2013; Griffin et al., 2004; Lambers et al., 2008; Takahashi et al., 2018; Valladares et al., 2002), but by no means universal. In dense forests with closed canopies, the removal of trees and the resulting sudden exposure to direct sunlight leads to photoinhibition, can lead to reduced A_{max}, and decreased growth in understory plants after disturbances like selective logging and drought (Kitao et al., 2018; Tng et al., 2022). In addition, although increased water availability to understory species (Fig 3) following overstory disturbance has been observed in northern hardwood forests, Mediterranean chaparral woodlands, and semi-arid coniferous biomes (Bearup et al., 2014; Dore et al., 2012; He et al., 2013; McIver et al., 2022; Mikkelson et al., 2013; Valladares & Pearcy, 2002), it also is not a universal response. In a PJ woodland in Mountainair, NM, for instance, piñon mortality led to aridification of the site and reduced physiological activity in the remaining trees. (Liebrecht, 2018; Morillas et al., 2017). In addition, ponderosa pine seedlings without canopy cover experience greater water stress during drought after severe fires (Bansbach, 2019). Thus, the factors that drive positive vs negative impacts of overstory mortality on sapling survival and success are still unclear.

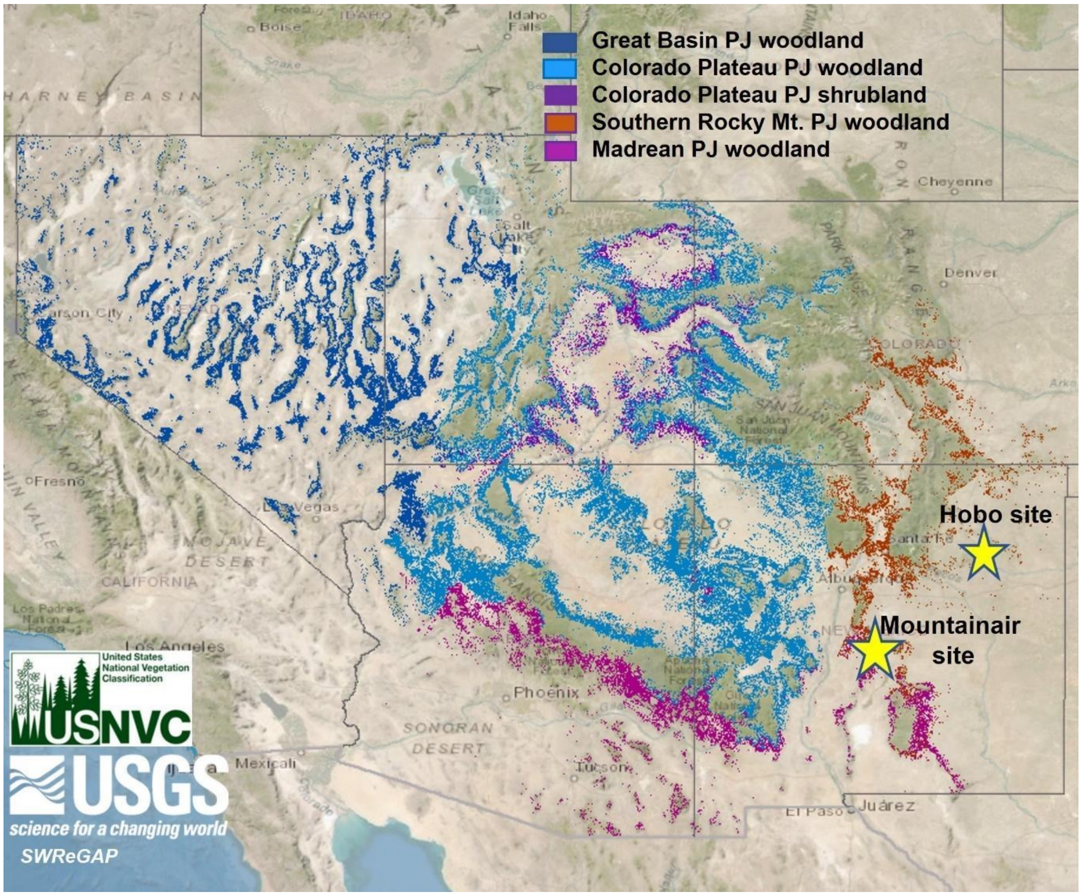
Redmond et al. (2018), emphasized that cooler and wetter climates, as well as soils with higher water retention capabilities, were key drivers in the resilience and success of PJ ecosystems following disturbances. Our site receives higher annual precipitation and the soils possess greater water-holding capacity due to the higher clay content compared to the Mountainair, NM study (Liebrecht, 2018; Morillas et al., 2017). These differences suggest that site-specific edapho-climatic conditions may dictate whether positive or negative responses to mortality are observed. Had we had conducted the study in a more stressful (drier) environment, the response could have differed based on facilitative plant-plant interactions being more prevalent in stressful environments, while competitive plant-plant interactions are more common in resource-rich environments (Bertness and Callaway, 1994).

The presence of nurse-trees providing favorable microclimates in PJ woodlands is essential for seedling recruitment and survival (Chambers, 2001; Mueller et al., 2005; Redmond et al., 2018). Surprisingly, both sapling species exhibited positive responses to loss of overstory as nurse plants, despite previous research indicating a connection between the presence of adult trees, emerging seedlings, and survival in PJ woodlands (Pirtel et al., 2021; Redmond et al., 2015, 2018). However, it is important to note that our study focused on well-established saplings prior to the girdling experiment, aligning with previous research highlighting the importance of advanced regeneration of juveniles for the resilience of these ecosystems (Redmond et al., 2018).

Environmental and Geographic Variability and Management Implications on PJ Woodland Resilience

PJ ecosystems exhibit significant variability in terms of species composition, landform and soil characteristics, and precipitation patterns, relative abundance and sizes of dominant species, and overall density of vegetation (USNVC ver. 2.03, SWReGap, 2005, Gedney et al., 1999, Springfield 1976, Jacobs, 2008). These woodlands are further classified into five distinct subtypes (Fig 9). This study was conducted in the Rocky Mountain PJ Woodland (Fig. 9), which is relatively mesic compared to southwest regions of this biomes range characterized by dry, rocky soils and harsher climates. This diverse range of characteristics across the northwest-to-southeast gradient (Romme et al., 2009) may dictate non-uniform responses with different constraints on recovery following overstory mortality. Specific environmental conditions, geographic location and PJ woodland subclasses should all be considered when assessing trajectory of responses to overstory mortality in PJ woodlands. It is important for land managers to understand and account for these dynamics when planning their implementation measures to mitigate the negative impacts of overstory mortality due to large-scale disturbance events such as drought stress, bark-beetle infestations, and fire. By recognizing these variations in ecophysiological responses, conservation efforts can be tailored to ensure the long-term health and sustainability of PJ woodlands across their entire range.

Figure 9. Map of southwest piñon-juniper woodlands subtypes illustrating the northwest to southeast gradient. Yellow stars represent the locations of our research site (Hobo) located within the Southern Rocky Mountain PJ woodland subtype and the research site from Liebrecht et. al, 2018 and Morillas et. al, 2017 (Mountainair) located within the Madrean PJ woodland subtype which represents the driest edge of this biomes range. This map was created using ESRI software (ArcMap 10.8.1).



Conclusions

The positive effects of overstory mortality on both piñon and juniper saplings suggest that in the absence of additional disturbance or climatic extremes, this site is likely to return to a PJ woodland. The fact that piñon saplings exhibited greater vulnerability in the aftermath of such mortality events, suggests an increased risk of woodland conversion to this biome to a juniper savanna, particularly in the hotter and drier climates in the drier edge of this biome's range. The disturbance response of saplings likely varies along a spectrum from net-negative to net-positive, and we expect that different PJ woodland types may exhibit diverse positions on this spectrum. Additionally, annual weather conditions, particularly wetter years, should influence the outcome of disturbances leaning towards more positive effects. These points highlight the necessity for future research on the physiological status of piñon and juniper saplings along a wider range of disturbance and climate regimes, as well as across different PJ woodland subclasses. Overall, these results deepen our understanding of the recovery trajectory in PJ biomes after significant die-offs and lead us to conclude that these woodlands may possess greater resilience than previously believed.

References Cited

Adams, H. D., Zeppel, M. J. B., Anderegg, W. R. L., Hartmann, H., Landhäusser, S. M., Tissue, D. T., Huxman, T. E., Hudson, P. J., Franz, T. E., Allen, C. D., Anderegg, L. D. L., Barron-Gafford, G. A., Beerling, D. J., Breshears, D. D., Brodribb, T. J., Bugmann, H., Cobb, R. C., Collins, A. D., Dickman, L. T., McDowell, N. G. (2017b). A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature Ecology & Evolution*, *1*(9), 1285–1291. https://doi.org/10.1038/s41559-017-0248-x

Allen, C. D., & Breshears, D. D. (1998). Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences*, *95*(25), 14839–14842. https://doi.org/10.1073/pnas.95.25.14839

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A., & Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, *259*(4), 660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Amiro, B. D., Barr, A. G., Barr, J. G., Black, T. A., Bracho, R., Brown, M., Chen, J., Clark, K. L., Davis, K. J., Desai, A. R., Dore, S., Engel, V., Fuentes, J. D., Goldstein, A. H., Goulden, M. L., Kolb, T. E., Lavigne, M. B., Law, B. E., Margolis, H. A., … Xiao, J. (2010). Ecosystem carbon dioxide fluxes after disturbance in forests of North America. *Journal of Geophysical Research*, *115*, G00K02. https://doi.org/10.1029/2010JG001390

Anderegg, W. R. L., & Anderegg, L. D. L. (2013). Hydraulic and carbohydrate changes in experimental drought-induced mortality of saplings in two conifer species. *Tree Physiology*, *33*(3), 252–260. https://doi.org/10.1093/treephys/tpt016

Baker, N. R. (1996). Photoinhibition of Photosynthesis. In R. C. Jennings, G. Zucchelli, F. Ghetti, & G. Colombetti (Eds.), *Light as an Energy Source and Information Carrier in Plant Physiology* (pp. 89–97). Springer US. https://doi.org/10.1007/978-1-4613-0409-8_7

Barszczowska, L., & Jędrysek, M. O. (2011). Carbon isotope distribution along pine needles (Pinus nigra Arnold). *Acta Societatis Botanicorum Poloniae*, *74*(2), 93–98. https://doi.org/10.5586/asbp.2005.013

Bearup, L. A., Maxwell, R. M., Clow, D. W., & McCray, J. E. (2014). Hydrological effects of forest transpiration loss in bark beetle-impacted watersheds. *Nature Climate Change*, *4*(6), 481–486. https://doi.org/10.1038/nclimate2198

Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., Romme, W. H., Kastens, J. H., Floyd, M. L., Belnap, J., Anderson, J. J., Myers, O. B., & Meyer, C. W. (2005). Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences*, *102*(42), 15144–15148. https://doi.org/10.1073/pnas.0505734102

Breshears, D. D., Nyhan, J. W., Heil, C. E., & Wilcox, B. P. (1998). Effects of Woody Plants on Microclimate in a Semiarid Woodland: Soil Temperature and Evaporation in Canopy and Intercanopy Patches. *International Journal of Plant Sciences*, *159*(6), 1010–1017. https://doi.org/10.1086/314083

Coplen, T. B. (2011). Guidelines and recommended terms for expression of stable-isotope-ratio and gas-ratio measurement results: Guidelines and recommended terms for expressing stable isotope results. *Rapid Communications in Mass Spectrometry*, *25*(17), 2538–2560. https://doi.org/10.1002/rcm.5129

Cregg, B. M. (1992). Leaf Area Estimation of Mature Foliage of Juniperus. *Forest Science*, *38*(1), 61–67. https://doi.org/10.1093/forestscience/38.1.61

Dore, S., Montes-Helu, M., Hart, S. C., Hungate, B. A., Koch, G. W., Moon, J. B., Finkral, A. J., & Kolb, T. E. (2012). Recovery of ponderosa pine ecosystem carbon and water fluxes from thinning and stand-replacing fire. *Global Change Biology*, *18*(10), 3171–3185. https://doi.org/10.1111/j.1365-2486.2012.02775.x

Duniway, M. C., Herrick, J. E., & Monger, H. C. (2010). Spatial and temporal variability of plant-available water in calcium carbonate-cemented soils and consequences for arid ecosystem resilience. *Oecologia*, *163*(1), 215–226. https://doi.org/10.1007/s00442-009-1530-7

Eitel, J. U. H., Vierling, L. A., Long, D. S., Litvak, M., & Eitel, K. C. B. (2011). Simple assessment of needleleaf and broadleaf chlorophyll content using a flatbed color scanner. *Canadian Journal of Forest Research*, *41*(7), 1445–1451. https://doi.org/10.1139/x11-058

Griffin, J. J., Ranney, T. G., & Pharr, D. M. (2004). Photosynthesis, Chlorophyll Fluorescence, and Carbohydrate Content of Illicium Taxa Grown under Varied Irradiance. *Journal of the American Society for Horticultural Science*, *129*(1), 46–53. https://doi.org/10.21273/JASHS.129.1.0046

Griffin, Monica Turner, & Martin Simard. (2011). Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone. *Forest Ecology and Management*, *261*(6), 1077–1089. https://doi.org/10.1016/j.foreco.2010.12.031

He, L., Ivanov, V. Y., Bohrer, G., Thomsen, J. E., Vogel, C. S., & Moghaddam, M. (2013). Temporal dynamics of soil moisture in a northern temperate mixed successional forest after a prescribed intermediate disturbance. *Agricultural and Forest Meteorology*, *180*, 22–33. https://doi.org/10.1016/j.agrformet.2013.04.014

Kitao, M., Harayama, H., Han, Q., Agathokleous, E., Uemura, A., Furuya, N., & Ishibashi, S. (2018). Springtime photoinhibition constrains regeneration of forest floor seedlings of Abies sachalinensis after a removal of canopy trees during winter. *Scientific Reports*, *8*(1), 6310. https://doi.org/10.1038/s41598-018-24711-6

Krause, G.H. (1988). Photoinhibition of photosynthesis. An evaluation of damaging and protective mechanisms. *Physiologia Plantarum*, *74*, 566–574. https://doi.org/10.1111/j.1399-3054.1988.tb02020.x

Lajtha, K., & Getz, J. (1993). Photosynthesis and water-use efficiency in piñon-juniper communities along an elevation gradient in northern New Mexico. *Oecologia*, *94*(1), 95–101. https://doi.org/10.1007/BF00317308

Liebrecht, A. I. (2018). *Linking Climate Change and Mortality in Piñon-Juniper Woodlands, from Leaf to Ecosystem*. https://digitalrepository.unm.edu/biol_etds/276

Limousin, J.-M., Bickford, C. P., Dickman, L. T., Pangle, R. E., Hudson, P. J., Boutz, A. L., Gehres, N., Osuna, J. L., Pockman, W. T., & Mcdowell, N. G. (2013). Regulation and acclimation of leaf gas exchange in a piñon-juniper woodland exposed to three different precipitation regimes: Rainfall manipulation in piñon-juniper woodland. *Plant, Cell & Environment*, *36*(10), 1812–1825. https://doi.org/10.1111/pce.12089

Llorens, L., Peñuelas, J., Beier, C., Emmett, B., Estiarte, M., & Tietema, A. (2004). Effects of an Experimental Increase of Temperature and Drought on the Photosynthetic Performance of Two Ericaceous Shrub Species Along a North-South European Gradient. *Ecosystems*, *7*(6). https://doi.org/10.1007/s10021-004-0180-1

Mackinney, G. (1941). ABSORPTION OF LIGHT BY CHLOROPHYLL SOLUTIONS. *Journal of Biological Chemistry*, *140*(2), 315–322. https://doi.org/10.1016/S0021-9258(18)51320-X

Marsh, C., Crockett, J. L., Krofcheck, D., Keyser, A., Allen, C. D., Litvak, M., & Hurteau, M. D. (2022). Planted seedling survival in a post-wildfire landscape: From experimental planting to predictive probabilistic surfaces. *Forest Ecology and Management*, *525*, 120524. https://doi.org/10.1016/j.foreco.2022.120524

Martínez-Vilalta, J., & Lloret, F. (2016). Drought-induced vegetation shifts in terrestrial ecosystems: The key role of regeneration dynamics. *Global and Planetary Change, 144*, 94–108. https://doi.org/10.1016/j.gloplacha.2016.07.009

McDowell, N.G., Beerling, D. J., Breshears, D. D., Fisher, R. A., Raffa, K. F., & Stitt, M. (2011). The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology & Evolution*, *26*(10), 523–532. https://doi.org/10.1016/j.tree.2011.06.003

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., & Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, *178*(4), 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

Mikkelson, K. M., Maxwell, R. M., Ferguson, I., Stednick, J. D., McCray, J. E., & Sharp, J. O. (2013). Mountain pine beetle infestation impacts: Modeling water and energy budgets at the hill-slope scale: PINE BEETLE IMPACTS ON THE WATER AND ENERGY BUDGET. *Ecohydrology*, *6*(1), 64–72. https://doi.org/10.1002/eco.278

Morillas, L., Pangle, R. E., Maurer, G. E., Pockman, W. T., McDowell, N., Huang, C.-W., Krofcheck, D. J., Fox, A. M., Sinsabaugh, R. L., Rahn, T. A., & Litvak, M. E. (2017). Tree Mortality Decreases Water Availability and Ecosystem Resilience to Drought in Piñon-Juniper Woodlands in the Southwestern U.S.: Tree Mortality in Semiarid Biomes. *Journal of Geophysical Research: Biogeosciences*, *122*(12), 3343–3361. https://doi.org/10.1002/2017JG004095

Norton, U., Ewers, B. E., Borkhuu, B., Brown, N. R., & Pendall, E. (2015). Soil Nitrogen Five Years after Bark Beetle Infestation in Lodgepole Pine Forests. *Soil Science Society of America Journal*, *79*(1), 282–293. https://doi.org/10.2136/sssaj2014.05.0223

Overpeck, J., & Udall, B. (2010). Dry Times Ahead. *Science*, *328*, 1642–1643.

Pirtel, N. L., Hubbard, R. M., Bradford, J. B., Kolb, T. E., Litvak, M. E., Abella, S. R., Porter, S. L., & Petrie, M. D. (2021). The aboveground and belowground growth characteristics of juvenile conifers in the southwestern United States. *Ecosphere*, *12*(11). https://doi.org/10.1002/ecs2.3839

Porra, R. J. (2005). The chequered history of the development and use of simultaneous equations for the accurate determination of chlorophylls a and b. In Govindjee, J. T.

Beatty, H. Gest, & J. F. Allen (Eds.), *Discoveries in Photosynthesis* (Vol. 20, pp. 633–640). Springer-Verlag. https://doi.org/10.1007/1-4020-3324-9_56

Porra, R. J., Thompson, W. A., & Kriedemann, P. E. (1989). Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophylls a and b extracted with four different solvents: Verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. *Biochimica et Biophysica Acta (BBA) - Bioenergetics*, *975*(3), 384–394. https://doi.org/10.1016/S0005-2728(89)80347-0

Rasband, W. S. (2018). ImageJ. Bethesda, MD: U.S. National Institutes of Health. Retrieved from https://imagej.nih.gov/ij/

Redmond, M. D., Cobb, N. S., Clifford, M. J., & Barger, N. N. (2015). Woodland recovery following drought-induced tree mortality across an environmental stress gradient. *Global Change Biology*, *21*(10), 3685–3695. https://doi.org/10.1111/gcb.12976

Redmond, M. D., Weisberg, P. J., Cobb, N. S., & Clifford, M. J. (2018). Woodland resilience to regional drought: Dominant controls on tree regeneration following overstorey mortality. *Journal of Ecology*, *106*(2), 625–639. https://doi.org/10.1111/1365-2745.12880

Reyer, C. P. O., Brouwers, N., Rammig, A., Brook, B. W., Epila, J., Grant, R. F., Holmgren, M., Langerwisch, F., Leuzinger, S., Lucht, W., Medlyn, B., Pfeifer, M., Steinkamp, J., Vanderwel, M. C., Verbeeck, H., & Villela, D. M. (2015). Forest resilience and tipping points at different spatio-temporal scales: Approaches and challenges. *Journal of Ecology*, *103*(1), 5–15. https://doi.org/10.1111/1365-2745.12337

Romme, W. H., Allen, C. D., Bailey, J. D., Baker, W. L., Bestelmeyer, B. T., Brown, P. M., Eisenhart, K. S., Floyd, M. L., Huffman, D. W., Jacobs, B. F., Miller, R. F., Muldavin, E. H., Swetnam, T. W., Tausch, R. J., & Weisberg, P. J. (2009). Historical and Modern Disturbance Regimes, Stand Structures, and Landscape Dynamics in Piñon–Juniper Vegetation of the Western United States. *Rangeland Ecology & Management*, *62*(3), 203–222. https://doi.org/10.2111/08-188R1.1

Royer, P. D., Breshears, D. D., Zou, C. B., Cobb, N. S., & Kurc, S. A. (2010). Ecohydrological energy inputs in semiarid coniferous gradients: Responses to management- and drought-induced tree reductions. *Forest Ecology and Management*, *260*(10), 1646–1655. https://doi.org/10.1016/j.foreco.2010.07.036

Royer, P. D., Breshears, D. D., Zou, C. B., Villegas, J. C., Cobb, N. S., & Kurc, S. A. (2012). Density-Dependent Ecohydrological Effects of Piñon–Juniper Woody Canopy Cover on Soil Microclimate and Potential Soil Evaporation. *Rangeland Ecology & Management*, *65*(1), 11–20. https://doi.org/10.2111/REM-D-11-00007.1

Royer, P. D., Cobb, N. S., Clifford, M. J., Huang, C.-Y., Breshears, D. D., Adams, H. D., & Villegas, J. C. (2011). Extreme climatic event-triggered overstorey vegetation loss increases understorey solar input regionally: Primary and secondary ecological implications: Extreme climatic event-triggered overstorey vegetation loss. *Journal of Ecology*, *99*(3), 714–723. https://doi.org/10.1111/j.1365-2745.2011.01804.x

Ryel, R. J., Ivans, C. Y., Peek, M. S., & Leffler, A. J. (2008). Functional Differences in Soil Water Pools: A New Perspective on Plant Water Use in Water-Limited Ecosystems. In U. Lüttge, W. Beyschlag, & J. Murata (Eds.), *Progress in Botany* (Vol. 69, pp. 397–422). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-540-72954-9_16

Schwinning, S., Litvak, M. E., Pockman, W. T., Pangle, R. E., Fox, A. M., Huang, C.-W., & McIntire, C. D. (2020). A 3-dimensional model of Pinus edulis and Juniperus monosperma root distributions in New Mexico: Implications for soil water dynamics. *Plant and Soil*, *450*(1–2), 337–355. https://doi.org/10.1007/s11104-020-04446-y

Stinziano, J. R., Roback, C., Sargent, D., Murphy, B. K., Hudson, P. J., & Muir, C. D. (2021). Principles of resilient coding for plant ecophysiologists. *AoB PLANTS*, *13*(5), plab059. https://doi.org/10.1093/aobpla/plab059

Tng, D. Y. P., Apgaua, D. M. G., Paz, C. P., Dempsey, R. W., Cernusak, L. A., Liddell, M. J., & Laurance, S. G. W. (2022). Drought reduces the growth and health of tropical rainforest understory plants. *Forest Ecology and Management*, *511*, 120128. https://doi.org/10.1016/j.foreco.2022.120128

USNVC (United States National Vegetation Classification) Database Ver 2.03. Federal Geographic Data Committee, Vegetation Subcommittee. Washington D.C. Accessed: November 20, 2022.

USGS National Gap Analysis Program. 2005. Southwest Regional GAP Analysis Project—Land Cover Descriptions. RS/GIS Laboratory, College of Natural Resources, Utah State University.

Valladares, F., Chico, J., Aranda, I., Balaguer, L., Dizengremel, P., Manrique, E., & Dreyer, E. (2002). The greater seedling high-light tolerance of Quercus robur over Fagus sylvatica is linked to a greater physiological plasticity. *Trees*, *16*(6), 395–403. https://doi.org/10.1007/s00468-002-0184-4

Villegas, J. C., Breshears, D. D., Zou, C. B., & Royer, P. D. (2010). Seasonally Pulsed Heterogeneity in Microclimate: Phenology and Cover Effects along Deciduous Grassland–Forest ContinuumAll rights reserved. No part of this periodical may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopying, recording, or any information storage and retrieval system, without permission in writing from the publisher. *Vadose Zone Journal*, *9*(3), 537–547. https://doi.org/10.2136/vzj2009.0032

West, A. G., Hultine, K. R., Sperry, J. S., Bush, S. E., & Ehleringer, J. R. (2008). Transpiration and Hydraulic Strategies in a Piñon-Juniper Woodland. *Ecological Applications*, *18*(4), 911–927. https://doi.org/10.1890/06-2094.1