# Mortality Thresholds of Juvenile Trees to Drought and Heatwaves: Implications for Forest Regeneration Across a Landscape Gradient

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# MORTALITY THRESHOLDS OF JUVENILE TREES TO DROUGHT AND HEATWAVES: IMPLICATIONS FOR FOREST REGENERATION ACROSS A LANDSCAPE GRADIENT

by

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As members of the Master's Committee, we certify that we have read the thesis prepared by: Alexandra Lalor
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and recommend that it be accepted as fulfilling the thesis requirement for the Master's Degree.

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Final approval and acceptance of this thesis is contingent upon the candidate's submission of the final copies of the thesis to the Graduate College.

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We respectfully acknowledge the University of Arizona is on the land and territories of Indigenous peoples. Today, Arizona is home to 22 federally recognized tribes, with Tucson being home to the O'odham and the Yaqui. Committed to diversity and inclusion, the University strives to build sustainable relationships with sovereign Native Nations and Indigenous communities through education offerings, partnerships, and community service.

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# ABSTRACT

Tree loss is increasing rapidly due to drought- and heat- related mortality and intensifying fire activity. Consequently, the fate of many forests depends on the ability of juvenile trees to establish following exposure to heightened climate anomalies. Climate extremes, such as droughts and heatwaves, are increasing in frequency and severity, and tree survival in mountainous regions must contend with these landscape-level climate episodes. Recent research focuses on how mortality of individual tree species may be driven by drought and heatwaves, but how mortality from protracted drought and associated warming would vary among multiple species spanning an elevational gradient given concurrent variation in climate, ecohydrology, and physiology remains unclear. We address this question by implementing a growth chamber study, imposing extreme drought with and without a compounding heatwave, for five species that span elevations across a semiarid elevational gradient in the southwestern United States. Overall, the length of a progressive drought required to trigger mortality differed by up to 20 weeks among species, whereas inclusion of a heatwave hastened mortality by about one week. Lower elevation species that grow in warmer ambient conditions died earlier (*Pinus ponderosa* in 10 weeks, *Pinus edulis* in 14 weeks) than did higher elevation species from cooler ambient conditions (*Picea engelmannii* and *Pseudotsuga menziesii* in 19 weeks, and *Pinus flexilis* in 30 weeks). When exposed to a heatwave atop drought, mortality advanced significantly only for species from cooler ambient conditions (*Pinus flexilis*: 2.7 weeks earlier; *Pseudotsuga menziesii*: 2.0 weeks earlier). Cooler ambient temperatures and associated differences in ecohydrology-related soil evaporation may have provided a buffer against moisture loss during drought, potentially overriding expected differences in drought tolerance due to tree physiology. Our study suggests that droughts will play a leading role in juvenile tree mortality and will most

directly impact species at warmer climate thresholds, with heatwaves atop drought potentially exacerbating mortality especially of high elevation species. These responses are relevant for assessing the potential success of both natural and managed reforestation, as differential juvenile survival following episodic extreme events will determine future landscape-scale vegetation trajectories under changing climate.

# INTRODUCTION

## Overview

*Pinus ponderosa* (ponderosa pine) is one of the most dominant and iconic tree species in the southwestern United States, yet the persistence of these forests is threatened by the expanding impacts of high-severity fires under conditions of climate change. Warming climates due to greenhouse gas emissions are causing forests to burn under high-severity conditions (Abatzoglou and Williams, 2016; Parks and Abatzoglou, 2020; van Mantgem et al., 2013). Drought stress is inducing widespread tree mortality, especially during the vulnerable early life stages of seedlings and saplings (Davis et al., 2019; Williams et al., 2012). Layering the challenges of high-severity fire and climate-induced tree mortality will continue to narrow regeneration opportunities for ponderosa pine forests.

Fire is a fundamental process which has historically shaped ponderosa pine forests in the southwest, evidenced by paleo-studies of tree rings extending back for millennia (Covington and Moore, 1994; Fulé et al., 1997, 2002; Margolis and Malevich, 2016; O'Connor et al., 2020). Ponderosa pines are well-adapted to low-intensity frequent fire intervals, with thick bark and tall canopies to survive returning fire every 1-10 years (Covington and Moore, 1994; Fulé et al., 1997). High-severity fires, defined as patches in which fire has killed greater than 75% of large overstory trees, were historically rare in this ecosystem (Covington and Moore, 1994; Margolis and Malevich, 2016). A century of fire suppression and subsequent fuel buildup has left forests in a drastically altered state, increasing risk of high-severity fire and diminishing the conditions which support low-severity fire (Covington and Moore, 1994; Westerling, 2006).

Compounding factors of warming temperatures, increased frequency of droughts, and widening extent of tree mortality will continue to play a role in future fire regimes (Allen et al., 2015; IPCC, 2021). Hotter drier climates are increasing the potential for severe wildfires (Chiodi et al., 2021; Davis et al., 2019; Holden et al., 2007; Mueller et al., 2020; Parks and Abatzoglou, 2020; Taylor et al., 2021; van Mantgem et al., 2013; Westerling, 2006; Williams et al., 2012). High-severity fires are unique in their fundamental alteration of stand structure and extensive tree mortality. These fires drastically alter soil properties such as nutrient content and hydrophobicity, leaving the landscape susceptible to erosion and hostile conditions for seedling recruitment (Cerdá and Doerr, 2005; DeBano, 2000; Dove et al., 2020). Such altered landscapes are primed for vegetation-cover shifts from forests to shrub-dominated landscapes (Loehman et al., 2020; O'Connor et al., 2020; Savage et al., 2013).

Ponderosa pine forests are facing numerous challenges under climate change and novel fire conditions. High-severity fire can restrict seedling growth by creating large gaps between seed-producing trees, allowing for resprouting shrubs to quickly establish, and producing hotter and drier soil microclimates which inhibit tree seedling growth. Climate change superimposes additional challenges to theses post-fire conditions, yet it is still unclear how seedling recruitment may response to these multiple stressors. Given the risks associated with high-severity fire for long-term forest loss, a critical measure of forest recovery will be determining levels of seedling establishment. Here, I assess current research of how post-fire seedling recruitment is limited by three factors – distance from seed sources, shrub density, and climate conditions – and how this research incorporates future climate into their analysis of post-fire forest recovery trajectories.

## Literature Review

I gathered a wide range of sources from Stevens-Rumann and Morgan (2019), a comprehensive review of tree regeneration following wildfires in the western United States, as a foundational source of information for the topic. From this study, I extracted papers specific to Arizona, New Mexico, and Colorado. I supplemented this with additional papers focused on seedling regeneration of ponderosa pine in southwestern states, in regions recovering from high-severity fires. In total, I reviewed 21 papers. I then structured my review around three factors limiting seedling regeneration following high-severity fire: distance from seed source, shrub density, and climate conditions.

### *Distance from Seed Source*

Seed-producing trees are necessary for conifer regeneration. As patches of high-severity fires become larger and more continuous, the distance between seed-producing trees and the interior patches becomes greater. Ponderosa pines have heavy seeds with a limited dispersal range, so these distances can become a formidable challenge (Chambers et al., 2016). Twelve papers reviewed explicitly considered distance from seed source as a limiting factor (Chambers et al., 2016; Coop et al., 2016; Haffey et al., 2018; Haire and McGarigal, 2010; Kemp et al., 2019; Malone et al., 2018; Owen et al., 2017; Rother and Veblen, 2016; Shive et al., 2013; Singleton et al., 2021; Stevens-Rumann et al., 2018; Ziegler et al., 2017). Increasing distance from seed producing trees was found to reduce the probability of seedling establishment in the majority of studies. Seed dispersal exhibited a maximum range of 300 m (Owen et al., 2017) but generally was concentrated within 200 m of seed-producing trees. As fires burn with larger high-severity effects and greater patch sizes, the ecological effects of reduced seed sources will become more profound.

Of the three papers that did not consider distance to seed source to be highly influential, results instead indicated stronger associations with topography (Ziegler et al., 2017), shrub density (Singleton et al., 2021), and climate (Kemp et al., 2019). One study found no differentiation between forest edge and core areas - defined as at least 200m from the forest edge (Singleton et al., 2021). Singleton et al. (2021), however, did find a negative correlation between shrub cover and regeneration, indicating that shrub density plays a more dominant role in regeneration dynamics. Another study used climate modeling to predict future seedling establishment, finding that warming climates will be the primary constraint on seedling establishment rather than distance from seed source (Kemp et al., 2019). This finding is particularly revealing, because it is unique in this review for using models of future climates to predict regeneration rather than using historic climate data to explain regeneration.

Importantly, eleven of these twelve studies focused on seedling regeneration from 1 to 30 years following fire, including eight studies focusing on less than 15 years. Ponderosa pine regeneration is generally slow and infrequent, with historic regeneration intervals of up to 40 years (White, 1985). Without longer scale studies, it is impossible to know the long-lasting effects of large high-severity patches on seedling regeneration.

### *Shrub Density*

Resprouting shrubs and trees are known to reproduce prolifically following high-severity fire (Minor et al., 2017). Shrubs also allow for deeper soil moisture infiltration following high-severity fire, which prevents erosion and furthers establishment (Cerdá and Doerr, 2005).

Additionally, the vegetation structure and volatile compounds in many shrubs facilitate more frequent high-severity fire regimes, after which shrubs can resprout and reestablish (Guiterman et al., 2018). Multiple effects of competitive growth and novel fire regimes may greatly inhibit ponderosa pine seedling regeneration in high-severity patches.

Of the papers reviewed, ten incorporated some measure of shrub density in their analysis (Coop et al., 2016; Guiterman et al., 2018; Haffey et al., 2018; Haire and McGarigal, 2010; Keyser et al., 2020; Roccaforte et al., 2012; Savage et al., 2013; Savage and Mast, 2005; Shive et al., 2013; Singleton et al., 2021). Of these, seven papers found shrub density to have a significant negative relationship to seedling density. In general, shrub density was found to be more frequent in high-severity burn sites and have a negative relationship with ponderosa seedlings, but the mechanisms underlying shrub competition were not analyzed. Underlying mechanisms are especially important when considering two dominant pathways of forest recovery found in this review – hyperdense regeneration and shrub conversion (Roccaforte et al., 2012; Savage et al., 2013; Savage and Mast, 2005). It is important to note that hyperdense ponderosa regeneration may not indicate long-term forest recovery, because hyperdense forests do not represent historic ponderosa forest structure and are prone to future high-severity crown fires (Savage et al., 2013). Future research on the competitive relationship between shrubs and ponderosa seedlings will aid in determining future forest trajectories.

The longer time scales of these studies could indicate future forest trajectories. Half were focused on longer term regeneration from 30-60 years, including one study which analyzed a 115-year-old post-fire shrub field. This indicates that shrubs may become a stable and long-lasting feature of high-severity fire landscapes.

### *Climate Conditions*

Climate conditions operate on a range of spatial scales, from the micro-climate of the post-high-severity landscape to climate change warming projections. At the micro-climate scale, high-severity fires create landscapes with lower soil albedo and more solar light penetration, which warms the soils surface and reduces soil moisture (Dove et al., 2020; McGuire and Youberg, 2019). Soils also become hydrophobic with intense heat, preventing water infiltration and limiting soil moisture (DeBano, 2000). At a macro-scale, climate change in the southwest U.S. is projected to cause increasing temperatures and increased intensity of extreme events, such as droughts (IPCC, 2021). Furthermore, hotter and drier climates are increasing the extent of high-severity fire – perpetuating the very problem I am investigating in this review (Westerling, 2006). Given the hotter and drier conditions of high-severity patches, these areas may become even more inhospitable with climate change. Thus, my categorization of "climate conditions" is intended to capture the hotter, drier conditions existing at multiple spatial scales.

Of the papers under review, ten explicitly considered the effects of climate on seedling regeneration, and nine of these studies identified as strong relationship (Davis et al., 2019; Feddema et al., 2013; Kemp et al., 2019; Malone et al., 2018; Rother et al., 2015; Rother and Veblen, 2016; Savage et al., 2013; Savage and Mast, 2005; Stevens-Rumann et al., 2018; Stoddard et al., 2018). Most studies found a combination of warmer and drier climates to influence seedling regeneration, while one study found that fall moisture specifically was a significant predictor (Feddema et al., 2013). These papers consider prior climate factors which contributed to observed seedling abundance, but do not project out to future climate conditions. Only two papers in this review consider the future climate projections on seedling recruitment, showing that climate thresholds for recruitment have already been crossed in some areas (Davis et al., 2019; Kemp et al., 2019). Rother et al. (2015) and Davis et al. (2019) show experimentally and through modeling that ponderosa seedlings are highly sensitive to warming temperatures, increased vapor pressure deficit, and limited water. Incorporating warming climates and project forest change with modeling studies will be crucial for extrapolating seedling regeneration into future scenarios.

### *Future Projections*

Modeling papers explicitly included management efforts into future scenarios of fire disturbances, climate change, and forest change over time. All these papers found that vegetation type-change transitioned from forest to shrubland in the long-term, regardless of management actions (Loehman et al., 2018, 2020; O'Connor et al., 2020). Prescribed fire reduced the likelihood of high-severity fire, but the warming temperatures eventually drove vegetation type-change despite management efforts (O'Connor et al., 2020). This lines up with findings by Stoddard et al. (2018), which found low seedling recruitment regardless of fire severity. This indicates that climate has a stronger role in seedling establishment than the unique challenges that high-severity fires pose. The rapidity of this finding is especially striking, with massive forest loss expected in the next 20-30 years even with elevated fuel reduction efforts (O'Connor et al., 2020).

## Discussion

The body of knowledge presented here demonstrates complex interactions between distance to seed source, shrub density, and climate as limiting factors for seedling recruitment. However, questions remain of how future climate scenarios will further impact successful seedling establishment. Most of these studies look at a short time scale, evaluating regrowth after 1-30 years following high-severity fire. This compressed time frame limits our understanding of regeneration, especially given the infrequent and sporadic nature of ponderosa regeneration (Mast et al., 1999; White, 1985). These studies also primarily focused on current or past climate data, without using predictive models to extend to future scenarios with warming climates. Many of these studies were conducted in the field, and climate impacts on seedlings have not been rigorously tested in controlled settings. Preliminary indicators suggest that climate will have a major effect on tree-mortality in the coming decades (Loehman et al., 2020; O'Connor et al., 2020). As forests across the southwest experience increased drought, hotter temperatures, and more severe fires, preserving our forests into the future will become critical. Thus, to predict future forest trajectories, there is a key research need to experimentally test how unprecedented climate changes will likely influence seedling establishment of not only ponderosa pine, but also other species across a common elevational gradient since collectively these will determine future vegetation dynamics across the landscape

# PRESENT STUDY

This thesis includes a manuscript intended for publication in a peer-reviewed journal, and is included as Appendix A. This manuscript, titled “Mortality thresholds of juvenile trees to drought and heatwaves: implications for forest regeneration across a landscape gradient” is intended for submission to *Frontiers in Forests and Global Change*. This research employs a growth chamber study approach to experimentally assesses how co-occurring climate extremes, such as droughts and heatwaves, may differentially impact juvenile trees of multiple species which span a semiarid elevational gradient.

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# **APPENDIX A:** MORTALITY THRESHOLDS OF JUVENILE TREES TO DROUGHT AND HEATWAVES: IMPLICATIONS FOR FOREST REGENERATION ACROSS A LANDSCAPE GRADIENT

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This article will be submitted to the journal *Frontiers in Forests and Global Change* for publication.

# MORTALITY THRESHOLDS OF JUVENILE TREES TO DROUGHT AND HEATWAVES: IMPLICATIONS FOR FOREST REGENERATION ACROSS A LANDSCAPE GRADIENT

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## Abstract

Tree loss is increasing rapidly due to drought- and heat- related mortality and intensifying fire activity. Consequently, the fate of many forests depends on the ability of juvenile trees to establish following exposure to heightened climate anomalies. Climate extremes, such as droughts and heatwaves, are increasing in frequency and severity, and tree survival in mountainous regions must contend with these landscape-level climate episodes. Recent research focuses on how mortality of individual tree species may be driven by drought and heatwaves, but how mortality from protracted drought and associated warming would vary among multiple species spanning an elevational gradient given concurrent variation in climate, ecohydrology, and physiology remains unclear. We address this question by implementing a growth chamber study, imposing extreme drought with and without a compounding heatwave, for five species that span elevations across a semiarid elevational gradient in the southwestern United States.

Overall, the length of a progressive drought required to trigger mortality differed by up to 20 weeks among species, whereas inclusion of a heatwave hastened mortality by about one week. Lower elevation species that grow in warmer ambient conditions died earlier (*Pinus ponderosa* in 10 weeks, *Pinus edulis* in 14 weeks) than did higher elevation species from cooler ambient conditions (*Picea engelmannii* and *Pseudotsuga menziesii* in 19 weeks, and *Pinus flexilis* in 30 weeks). When exposed to a heatwave atop drought, mortality advanced significantly only for species from cooler ambient conditions (*Pinus flexilis*: 2.7 weeks earlier; *Pseudotsuga menziesii*: 2.0 weeks earlier). Cooler ambient temperatures and associated differences in ecohydrology-related soil evaporation may have provided a buffer against moisture loss during drought, potentially overriding expected differences in drought tolerance due to tree physiology. Our study suggests that droughts will play a leading role in juvenile tree mortality and will most directly impact species at warmer climate thresholds, with heatwaves atop drought potentially exacerbating mortality especially of high elevation species. These responses are relevant for assessing the potential success of both natural and managed reforestation, as differential juvenile survival following episodic extreme events will determine future landscape-scale vegetation trajectories under changing climate.

## Introduction

Droughts and heatwaves are expected to increase in frequency and magnitude with changing climate (IPCC, 2021), acting in concert to increase tree mortality in forests around much of the globe (Allen et al., 2015; Hammond et al., 2022). Increased evapotranspiration and early spring snowmelt are expected to lengthen dry periods, causing surface soil moisture deficits and prolonged regional drought (Abatzoglou and Williams, 2016; IPCC, 2021; Williams et al., 2022). Heatwaves (defined as three or more consecutive days of elevated temperature above the 90th percentile of the seasonal mean) are also projected to become more frequent and intense (Steffen et al., 2014). Globally, one to six extra heatwave days have occurred each decade since 1950 (Perkins-Kirkpatrick and Lewis, 2020). Long duration heatwaves have also increased from five days in 1950 to an average of seven days in 2017 (Perkins-Kirkpatrick and Lewis, 2020; Fig 3b). Evidence of tree die-off events related to hotter droughts have been observed globally (Allen et al., 2015; Hammond et al., 2022). Additional observational evidence indicate that heatwaves amplify tree mortality under drought conditions (Matusick et al., 2018; Niinemets, 2010; Ruthrof et al., 2018).

In the southwestern United States, drought and warming is likely to be particularly pronounced. This region is currently in a megadrought, projected to exceed the worst drought event since 800 CE in both duration and severity (Williams et al., 2022, 2020). Droughts lasting five weeks in duration have occurred more than sixty times in the last hundred years (Adams et al., 2009; Fig 3). In southwestern woodlands, soil water content measurements over 15 years shows that soil moisture can remain low for an entire year, as it did during the 2002 drought (Breshears et al., 2009; Fig A1). As drought duration and severity in the southwest are expected to increase, the same is expected for hot extremes (IPCC, 2021; Fig 3). Under regionally downscaled climate projections from ten CMIP5 models of a 4°C temperature increase by the end of century in the southwest, the probability distribution functions for extreme heat is expected to shift towards hotter heatwave events, with extreme temperatures of about 10°C above current means possible (Guirguis et al., 2018; Fig 3i).

Co-occurring climate stressors such as drought and heatwaves (along with associated impacts from pests and pathogens; Simler-Williamson et al., 2019) have the potential to cause tree mortality across broad regions. Large scale tree mortality events in the southwest have been observed in response to drought alone (Allen and Breshears, 1998) and to drought and chronic warming (Breshears et al., 2005). The potential for rapid tree mortality is especially significant given increasing forest loss from recent fire-climate interactions that have driven increases in both wildfire area and severity (Allen, 2014, 2009; Coop et al., 2016; Falk, 2013; Singleton et al., 2019). Fire interactions with regional drought and warming temperatures have contributed to unprecedented forest loss in historically fire-tolerant ecosystems (Abatzoglou and Williams, 2016; Guiterman et al., 2022; Parks and Abatzoglou, 2020; van Mantgem et al., 2013). Landscape-scale models incorporating ecosystem-fire processes predict extensive forest loss across landscapes by the end of the century (Loehman et al., 2020), with southwestern forested area expected to decline in the coming decades in many areas (McDowell et al., 2016; O'Connor et al., 2020).

Tree mortality at young growth stages is especially relevant to forest recovery following adult tree mortality from drought-related die-off (Batllori et al., 2020; Redmond et al., 2018) and from wildfire (Stevens-Rumann et al., 2022). Forest recovery depends first on successful recruitment of new seedlings, and then the survival of those seedlings to reproductive age. Successful recruitment of new seedlings can be limited by lack of seed sources or inhospitable growing conditions, which can be especially prevalent in post-disturbance landscapes such as after high-severity fires (Ibáñez et al., 2021; Nolan et al., 2021; Stewart et al., 2021). Establishing seedlings must also outcompete emerging plant communities for nutrients and water (Fenner, 2000). Drought-related tree mortality can alter forest age structure at a broad scale and reset successional progression, opening up resources for competing species (Clifford et al., 2011). Widespread tree-mortality can also potentially cause woodland to savannah conversions

(Clifford et al., 2011), or the replacement of mesic trees with more xeric tree and shrub communities (Batllori et al., 2020). Even with successful seedling establishment, post-disturbance tree survival can be precarious for multiple years (White, 1985), and survival may be further impeded by subsequent climate extremes (Kemp et al., 2019). Previous studies have addressed seedling recruitment under changing climate (Bailey et al., 2021; Davis et al., 2019; Kemp et al., 2019; Nelson et al., 2021; Stewart et al., 2021), yet few have examined drivers of mortality in well-established juvenile trees (Rother and Veblen, 2016). In southwestern woodlands where large-scale tree dieback events have occurred, regeneration capacity improved with the survival of juvenile trees (Redmond et al., 2018). Focusing of juvenile survival in the face of recurring climate disturbances can further inform the recovery potential of tree species.

Predicting how tree juveniles across a landscape will respond to singular or compounded climate extremes (e.g. drought or drought with a co-occurring heatwave) is dependent on three interacting factors which vary across elevational gradients: (1) species and their ecophysiological adaptations, (2) ecohydrological influences, and (3) temperature influences. First, species vary across an elevational gradient and have specific physiological adaptations to survive in their bioclimatic range. These adaptations, such stomatal regulation to avoid hydraulic failure or carbon starvation (McDowell et al., 2008), allow species to respond differentially to potential mortality drivers (Koepke et al., 2010). Second, ecohydrological influences of tree structure on its environment also differentially affect water availability; more open tree structures allow greater evapotranspiration and water loss, while more dense canopy structures can shade soil and retain moisture (Royer et al., 2012). As vegetation communities shift over landscapes, the interaction between canopy structure and soil moisture can attenuate or accentuate drought impacts across species. Third, temperatures vary across elevations, where lower elevations broadly correspond to warmer temperatures and increased evaporation rates (Haire et al., 2022). Individuals within a species which are acclimated to growing in warm, dry environments are expected to have a broader tolerance for climate extremes such as heat and drought (Ahrens et al., 2021). Yet other studies suggest that such adaptations do not afford species greater tolerance to heatwaves (López et al., 2022; Notarnicola et al., 2021). These co-occurring factors of differing species ecophysiology, ecohydrological interactions, and temperature gradients across elevations make predicting differential responses among multiple species difficult to assess without controlled experimentation.

Species tolerance to mortality drivers can be detected observationally by leaf browning trends, reflecting chlorophyll degradation and loss of photosynthetic capacity (Jong et al., 2012; Myneni et al. 1995). Prior studies have used ocular estimates of percent brown to quantity the timing to mortality (Adams et al., 2017, 2009), but image analysis might enable more consistent, quantitative, repeatable, and precise metrics to asses color continuum change.

Uncertainty in forest recovery potential has prompted extensive studies of post-fire seedling regeneration in post-fire landscapes - whether from natural regeneration or replanting from nursery stock (Chambers et al., 2016; Owen et al., 2017; Roccaforte et al., 2012; Ziegler et al., 2017). Without successful tree regeneration, high-severity patches in post-fire landscapes are vulnerable to reorganization, including vegetation type conversion, at a landscape scale (Falk et al., 2022; Savage et al., 2013). Outplanting of juvenile trees that have been raised as nursery stock has been implemented strategically to reforest disturbed landscapes in the southwest (Stevens et al., 2021). Land managers reforesting landscapes may be especially interested in juvenile tree responses to climate extremes, considering how outplanting success relates to tree size and species stress tolerance (Andivia et al., 2021). To address how landscapes will respond to disturbances of adult tree die-off from drought and wildfire, we need to understand how juveniles of multiple species that span those landscapes will fare in subsequent expected extreme events, likely including droughts and heatwaves.

Our goal was to experimentally assess relative tolerance of five tree species at the juvenile growth stage to the imposition of drought and heatwaves in a controlled environment. We focused on a suite of species found across elevations in the Jemez Mountains of New Mexico, a model study area for vegetation change in response to drought and warming (Allen and Breshears, 1998; Breshears et al., 2005; McDowell et al., 2019) and wildfire (Coop, 2022; Coop et al., 2020; Guiterman et al., 2022, 2018; Haire et al., 2017; Haire and McGarigal, 2010). We designed an experiment to evaluate how prolonged drought, with and without heatwave exposure, may influence juvenile tree survival for five tree species that occur in this area. More specifically, we hypothesized that a protracted drought could trigger differential mortality of tree species, as occurred in 2002 in the southwest (Gitlin et al., 2006). We asked two primary questions: (1) what are the differences in time to mortality among species under prolonged drought? And (2) does the additional imposition of a heatwave alter the time to mortality within these species? We hypothesized that: (1) species characteristic of different elevation zones would have different responses to drought stress due to a combination of species ecophysiology, ecohydrological influences, and temperature influences; and (2) within species, individuals exposed to a co-occurring stressor of a heatwave atop drought will die more quickly than individuals without heatwave exposure. Our approach for addressing this was to implement growth chamber studies where we could impose extreme drought with and without a compounding heatwave for multiple species spanning an elevational gradient.

## Methods

### *Study Area and Tree Species Selection*

We selected our species and climate conditions in the context of the Jemez Mountains, located in northern New Mexico, USA (36°N, 106°W). The Jemez Mountains have a semi-arid continental climate and have been the site of numerous studies on drought-and heat-related tree mortality (Allen et al. 1998; Breshears et al. 2005, 2009, Rich et al. 2005, McDowell et al. 2019). The landscape has also experienced extensive change from uncharacteristic high-severity wildfires (Allen, 2007). Forest soils are composed of volcanic rock and gravel with a loam texture, dating mostly to Pleistocene eruptions that created the dominant physiographic feature of the range, a prominent crater known as the Valles Caldera (Muldavin and Tonne, 2003; Soil Survey Staff et al., 2002). Across the Jemez Mountains, mean annual precipitation (1991-2020 norm) is 564 mm with a majority (214 mm) falling in the summer monsoon season from July to September (Hegewisch and Abatzoglou, 2022). Highest average summer temperatures (7.8 to 24.3°C) and lowest rainfall (27.4 mm) are in June, the most likely time for prolonged drought and heatwave conditions (Hegewisch and Abatzoglou, 2022). The elevational range of the Jemez Mountains extends from 1,800 m to 3,500 m, supporting ecological communities across elevations from piñon-juniper woodlands to dense spruce-fir forests (Johnson, 2001). Ecological communities across the mountain range have been exposed to an extensive history of low-intensity fires, documented by tree ring records across the Jemez (Dewar et al., 2021), before being interrupted in the late 1800s by a century of overgrazing and fire suppression (Margolis and Malevich, 2016). High-severity fires have characterized the landscape in recent decades, raising uncertainty about patterns of forest regrowth and recovery (Guiterman et al., 2022; Stevens et al., 2021).

To compare juvenile tree vulnerability as an indicator of forest recovery potential, we selected five study species that are dominant or co-dominant in mid- to upper-elevation forest communities across the Jemez Mountains. Species were selected both for their relative dominance within elevational zones and for their availability in tree nurseries in the western United States, which are a primary source of plant material for active reforestation management (Landis et al., 2010). Our selected species were *Pinus ponderosa* Douglas ex Lawson & C. Lawson (ponderosa pine), *Pinus edulis* Engelmann (piñon pine), *Pinus flexilis* E. James (limber pine), *Pseudostuga menziesii* Mirbel Franco (Douglas fir), and *Picea engelmanni* Engelmann (Engelmann spruce)[1]. Within the Jemez Mountains, *Picea engelmanni* occurs most frequently in cooler, wetter sites at upper elevations of 3,000 meters (10,000 ft). *Pinus flexilis* and *Pseudostuga menziesii* occur in slightly drier sites above 2,900 meters (9,500 ft). At the lowest forest elevational range, *Pinus ponderosa* and *Pinus edulis* occur in open forests and forest-woodland ecotones, at mean elevations of 2,590 meters (8,400 ft) (Muldavin and Tonne, 2003).

We developed temperature profiles for each species to establish ambient temperature conditions for experimental chambers. We used detailed 1987 vegetation surveys across the Jemez landscape (Allen et al., 1989) to determine the elevation range for each species. We derived mean daily minimum and maximum temperatures from PRISM (Climate PRISM Group, Oregon State University) using all the location occurrences in that study for each of the species. PRISM weather data were derived between the years 1970 to 2000, with a spatial resolution of 4 km, for the month of June, historically one of the warmest months for this landscape (Bowen et al. 1990). We defined our lower elevation ambient temperature regime where *Pinus ponderosa*

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[1] Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico [Online]. 22+ vols. New York and Oxford. http://beta.floranorthamerica.org. Accessed November 17 2022.

and *Pinus edulis* co-occur as warm, dry forest types in the Jemez. Where cooler, wetter forests support a mix of *Picea engelmanni*, *Pseudostuga menziesii*, and *Pinus flexilis*, we defined our higher elevation ambient temperature regime (Bowen et al., 1990). Temperatures were set to fluctuate between minimum and maximum temperatures, following a diurnal pattern, and heatwaves were calculated as a 10°C increase over these ambient temperature patterns (Table 1; Figure 1).

Three temperature-controlled plant growth chambers (Conviron, Model E7/2, Pembina North Dakota, USA) were set to temperatures that matched the PRISM data for each species or species group. The growth chambers received 12 hours of visible light (400 to 700nm wavelengths) at a total output of 7,180 lumens from Agrobrite compact fluorescent light bulbs in each 24-hour diurnal cycle. The fourth chamber was used to implement a one-week heatwave for a subset of plants in each chamber (staggered in time as detailed below in *Experimental Design*). The high elevation group was divided into two chambers, one containing *Pinus flexilis* and *Pseudostuga menziesii*, and the other containing *Picea engelmanni*. We calibrated chamber temperatures using two Kestrel weather instruments (Kestrel 5500, Nielsen-Kellerman, USA) placed on either end of each chamber to measure temperature accurately and ensure consistency across chambers. Both chambers achieved near identical temperature fluctuations and heatwave increases, with average temperatures deviating 0.3 – 0.5°C from the target temperatures. We maintained the heatwave chamber to +10°C (actual range 8.9-10°C) above each species' ambient temperature.

### *Experimental Design*

We acquired fifty individuals per species as a target sample size, plus additional plants to account for mortality during transportation and transplanting. *Pinus edulis* and *Pseudostuga menziesii* were purchased from the University of Idaho's Franklin H. Pitkin Forest Nursery in Moscow Idaho, USA. *Picea engelmanni*, *Pinus ponderosa*, and *Pinus flexilis* were purchased from the Colorado State Forest Service Nursery in Fort Collins Colorado, USA. Trees had well-established root systems and are consequently referred to in this study as juveniles, which represent individuals that have progressed beyond the seedling stage (first one to two years of initial growth following seed germination and initial root and shoot development), but prior to the sapling stage (established trees > 1 m tall) (Burrill, 2021; Fenner, 2000; National Park Service, 2003). Juvenile trees used in this experiment averaged 4 ± 0.9 years old at the beginning of the experiment (Table 3).

All plants arrived in April 2021 and were placed into a temporary electric growth chamber set to a constant 15°C with 12 hours of fluorescent light per 24-hour diurnal cycle. Plants were watered regularly to maintain non-limiting soil moisture. All individuals were moved from the growth chamber to the greenhouse in May 2021 with a daytime high temperature of 29°C and a nighttime low temperature of 10°C. After one month of acclimation to the greenhouse, the plants were repotted into 10 x 10 x 35 cm pots in June 2021. Soil was mixed to roughly replicate an intermediate textured soil type, in terms of sand, silt and clay composition, of the Jemez Mountains, using sandy loam soil (Acme Sand and Gravel, Tucson, AZ, USA) sieved to a gravel size of 2mm and amended with 30% pure sand and 25% sphagnum peat moss based potting soil (Sunshine Mix #4, Sungro Horticulture, Agawam, MA, USA).

We hypothesized that juveniles of different species would die at varying rates under climate conditions of prolonged drought, and that mortality rates would increase when exposed to an acute heatwave. Timing, duration, and magnitude of heatwave are all variables of potential interest but must be constrained within a single study. Our heatwave parameters (+10°C above ambient temperature for seven days) are meant to test the extremes of modeled heatwave probabilities in the southwest (Guirguis et al., 2018). The duration and intensity of our heatwave is consistent with experimental propositions to test heatwaves effects, severe enough to elicit responses in plant mortality but within the realm of possibility for expected heatwave events (Breshears et al., 2021; Perkins-Kirkpatrick and Lewis, 2020). We selected a magnitude of 10°C above ambient temperatures with a duration of one week, which has been proposed as a target for initial studies of heatwaves to enable cross-study comparisons (Breshears et al. 2021). We selected seven weeks into the study to implement the heatwave, which approximates a range of time between when peak soil moisture is likely to occur in late spring and when hotter summer temperatures begin to occur in the study area (e.g. for soil moisture dynamics in *Pinus edulis* woodlands; see Breshears 2009 Fig. A1). This heatwave study expands upon previous studies that had tested heatwaves of 5-7°C increase over ambient for 5-6 days (Marchin et al., 2022; Notarnicola et al., 2021). We expand our scope beyond these prior studies to explore heatwave effects on higher elevation species with lower ambient temperatures (Table 2).

To implement the experiment, fifty individual plants per species were assigned randomly to two treatment groups: a *temperature treatment*, an a *water treatment*. Within the temperature treatment group, twenty-five individuals per species were assigned randomly to absence or occurrence of a heatwave. Plants remained under ambient temperature conditions within their growth chamber, except that individuals within the heatwave treatment were exposed to a 10°C above ambient increase for seven days during week seven of the experiment before being returned to ambient temperature conditions. In each temperature treatment, the majority (*n* = 20) received no additional water for the duration of the experiment, while a subset of individuals (*n* = 5) was watered to saturation every two weeks to enable us to confirm whether drought was driving juvenile mortality.

We used a staggered-in-time design to expose each species to a heatwave during week seven, given our restriction that only a single chamber was available for implementing heatwaves. The start of the experiment was staggered by two weeks between each of the other three chambers, meaning that "Week 1" of the experiment corresponds to different calendar dates for each chamber. This allowed sufficient time and space to prepare the heatwave chamber for each round of heatwaves. Plants were placed into the growth chambers in August and September 2021. All plants were watered fully and fertilized at the beginning of the experiment (Week 0), and measurements began at Week 1. Fertilizer was applied as instructed: about 29.6 grams of Liquinox All-Purpose Fish Fertilizer (NPK 5-1-1) mixed with 3.78 liters of water. Each plant was watered to saturation and then 0.3 liters of fertilizer mixture was sprayed onto the soil with a chemical sprayer. Midway in Week 3, containers with 297 grams of calcium chloride desiccant (Damp Rid, W.M. Barr, Memphis, TN, USA) were used to offset the humidity increase associated with watering treatments. Two desiccant containers per species were placed in each chamber, monitored weekly and refilled as needed. At week five, the foliage of all plants was saturated with insecticidal soap (Bondie Products LLC, Oriskany, NY, USA) to treat a mild occurrence of scale insect (*Adelges sp.*) [Hemiptera: Adelgidae] on our *Pinus ponderosa* species.

*Measurements*

Tree size was characterized by taking single measurements of height (mm), basal diameter (mm), and dry weight biomass (g); these were taken over the course of the experiment, assuming tree biomass did not change substantially given that they were droughted (Table 3). Age was estimated using branch whorl counts (Husch et al., 2003). Height was measured from the soil surface to the apical bud, and basal stem diameter was measured with a metric caliper at the base of each tree. Biomass was measured at the end of the experiment once all trees had died. Individuals were clipped at the base, placed into labeled brown paper bags, set in a drying oven set at 75°C for 24 hours, and weighed.

We took weekly measurements capturing three key potential drivers of plant stress: (1) water availability, (2) stomatal conductance, and (3) leaf browning assessed using ocular estimates and photos.

First, to measure water availability and soil water loss, we weighed plants gravimetrically (grams) each week. Water stress was calculated as an inflection point along a water loss curve, reflecting an estimate of when water availability transitions from relatively non-limiting to relatively limiting resource (van Genuchten, 1980). Water loss curves for each plant were constructed using weight data; inflection points were calculated using R to compute the second derivative of the curve to find changes in concavity. Curves were inspected visually to isolate the soil water content inflection point (Figure 4).

Second, we measured stomatal conductance (mmol $m^{-2}s^{-1}$) on the uppermost needles of a subset of juveniles ($n$ = 3 watered, 10 droughted) using a leaf porometer weekly (Model SC-1, Meter group, Pullman, Washington, USA) as an indicator of plant transpiration. Low conductance measurements indicate that plant transpiration is reduced (Marchin et al., 2022).

Because conductance measurements of non-conducting tissue (dry filter paper) recorded a minimum value of 90 mmol $m^{-2}s^{-1}$, we assumed that plants had reached permanent stomatal closure when conductance was consistently at or below this minimum value (Figure 5).

Third, to establish a mortality date, we visually inspected leaf color twice per week to record leaf browning. Leaf color change from green to brown represents the breakdown of chlorophyll within plant cells. Ocular estimates of 90% brown thresholds have been used as a benchmark to determine plant death in other mortality studies (Adams et al., 2017, 2009). We categorized percent brown as 10%, 25%, 50%, 75%, or 90% brown. Because we observed that many plants retained their green color even while exhibiting other signs of severe tissue degradation, we also used criteria related to needle loss and brittleness (needles that broke under slight pressure) to help establish time of mortality. Plants were declared dead when they reached a 90% threshold for percent brown, needle loss, or brittle needles. As a metric of mortality, foliar color has been shown to relate to hydraulic failure, although this response is lagged for the one species of *Pinus* in that study (*Pinus radiata* D. Don; Blackman et al., 2019); a less temporally detailed analysis also documented a lagged response in a second species: *Pinus taeda* Linnaeus (Hammond et al. 2019). We continued to measure individuals for two weeks after their death date to confirm each mortality event; the experiment concluded when all droughted plants died, given that watered plants were not expected to die.

To expand upon ocular estimates of leaf color, we developed an image analysis approach for quantitative, repeatable, and precise metric assessing color continuum change (e.g. Hammond et al., 2019). This method has the potential to measure leaf color across a continuum to assess overall changes in leaf browning over time. Photographs were taken weekly against a grey background in the same position and with similar lighting (white balance of 3200-3400 K) using a digital camera (Sony Alpha 6000 mirrorless, 24.3-megapixel 16-50 mm zoom lens). We developed Python code[2] to separate photo pixels into background colors and plant colors (RGB), using the LAB (lightness) color channel to determine thresholds between plant and background pixels (Van Rossum and Drake, 2009). The R package *colorfindr* was then used to summarize plant color information into red (~700nm), green (~550nm), and blue (~470nm) pixel values and graph colors on three-dimensional RGB axes, measured on a scale of 0 to 255 (unitless) (R Core Team, 2022; Zumbach, 2019). To quantify leaf senescence based on pixel color, we used red, green, and blue pixel values to pool a continuum of colors into discrete categories of green and brown, which could be compared against ocular estimates. We categorized pixels as "brown" (~600nm) where the red value was greater than the green value, and "green" (~550nm) where the green value was greater than the red value.

### *Statistical Analyses*

We analyzed significant differences in time to mortality within each species using two-sample *t*-tests in two contexts. First, we verified our control group to ensure that juvenile death was attributed to drought rather than chamber conditions, testing for differences between watered and droughted juveniles within each species. Second, we tested for differences in heatwave effects among droughted juveniles within each species. We visually inspected for normality and used Shapiro-Wilk tests to compare raw and transformed data and determined that untransformed data met the assumptions of normality (Shapiro and Wilk, 1965). We performed statistical tests with and without outlier data points; because outliers did not change statistical conclusions, we included outliers in the final analysis. Using a two-sample *t*-test, we evaluated the null

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[2] https://github.com/DevinBayly/Allie_plant_segmenting

hypothesis that juveniles within a species would respond equally to drought, with or without heatwave exposure. The alternative hypothesis is that juveniles with exposure to a heatwave would have more rapid mortality rates. Because juveniles with heatwave exposure were expected to die more quickly on average, a one-sided *p*-value was used to evaluate significance (alpha = 0.05).

We used a one-way ANOVA to test significance of time to mortality among species. We compared individuals within drought-only treatment groups, and separately compared individuals within drought-heatwave treatment groups. We compared sample sizes and variance of data to determine that our data fit ANOVA assumptions. Data were analyzed using three measures of time to mortality, as indicators of drought stress: time to mortality (in weeks) since (1) water restriction, at the beginning of the experiment; (2) water stress, calculated from weight data as a water loss inflection point; and (3) permanent stomatal closure, when conductance data consistently reached a minimum. Across these three measures, we evaluated the null hypothesis that all species would respond equally to drought and have the same time to mortality. The alternative hypothesis is that at least one species mortality rate would differ. Given that mortality rates differed among species, further post-hoc analysis of species differences were tested using Tukey's honest significant difference (HSD). We graphed predicted survival probability against observed values using the R package *survival* to produce a Kaplan-Meier curve, a nonparametric estimation of survival (Kaplan and Meier, 1958).

All statistical analyses and visualizations were completed using R Statistical Software, version 4.2.1 (R Core Team, 2022) and figures were produced using the package *ggplot2* (Wickham 2016). All code is available on publicly available GitHub pages[3].

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[3] https://github.com/alexandralalor/HeatwaveProject

## Results

### *Survival of Watered Juveniles*

Our experimental focus was on drought effects with and without a heatwave, so we used our set of watered juveniles as a control group to confirm drought effects as the driver of mortality. We followed the progression of juvenile death until 100% of droughted individuals reached mortality. In the time that all droughted individuals had died, watered juveniles of four species (*Picea engelmannii*, *Pinus edulis*, *Pinus flexilis,* and *Pseudotsuga menziesii*) had 0% mortality. One of five watered *Pinus ponderosa* individuals died in both the ambient and heatwave groups. The number of juveniles that died during the experiment was statistically different between watered and droughted *Pinus ponderosa* juveniles (two-sample *t*-test, $t_{48} = -12.39$, one-sided $p < 0.0001$). Collectively, these results validate that conditions within the growth chambers were suitable for juvenile growth if water is not limiting.

### *Species Differences*

We focused our primary analysis on species responses to prolonged drought. Under ambient temperatures and drought conditions, average time to mortality differed among species (analysis of variance *F*-test, $F_{4,94} = 256.6$, $p < 0.0001$). *Pinus ponderosa* tree juveniles died most quickly ($\bar{y} = 10.7$ weeks, SD = 1.71, $n = 20$), followed by *Pinus edulis* ($\bar{y} = 14.6$ weeks, SD = 2.17, $n = 19$), *Picea engelmannii* ($\bar{y} = 19.2$ weeks, SD = 1.51, $n = 20$), *Pseudotsuga menziesii* ($\bar{y} = 19.4$ weeks, SD = 2.31, $n = 20$), and *Pinus flexilis* ($\bar{y} = 30.3$ weeks, SD = 2.39, $n = 20$). All species were significantly different from each other, except for *Picea engelmannii* and *Pseudotsuga menziesii* (post-hoc Tukey HSD test; Table 5a). These contrasts did not change when analyzing species under the drought-heatwave treatment (post-hoc Tukey HSD test; Table

5a). Using a Kaplan Meier survival function, we plotted a predicted survival probability curve against observed values for each species (Figure 3).

### *Heatwave Effects*

Our secondary analysis was focused on species responses to a weeklong heatwave event overlapping the experimentally imposed drought. Among all species, the mean time to mortality was earlier among juveniles with heatwave exposure (0.3 to 2.7 weeks earlier than drought-only juveniles), although this difference was not statistically significant for either of the lower elevation species (*Pinus ponderosa*, *Pinus edulis*) (Figure 2, Table 4).

Two of three higher elevation species exposed to a heatwave had statistically significant shorter time to mortality (*Pinus flexilis*, *Pseudotsuga menziesii*). *Pinus flexilis* individuals with a heatwave treatment ($\bar{y} = 27.6$, SD = 5.05, $n = 20$) died an average of 2.7 weeks before those with no heatwave treatment ($\bar{y} = 30.3$, SD = 2.39, $n = 20$) (two-sample *t*-test, $t_{38} = -2.16$, one-sided $p = 0.018$), and *Pseudotsuga menziesii* juveniles with a heatwave treatment ($\bar{y} = 17.4$, SD = 2.39, $n = 20$) died an average of 2.0 weeks before those with no heatwave treatment ($\bar{y} = 19.4$, SD = 2.31, $n = 20$) (two-sample *t*-test, $t_{38} = -2.69$, one-sided $p = 0.005$).

### *Time To Mortality Adjusted to Metrics of Stress Onset*

Across all species, we found that water stress was the earliest stress indicator (Figure 4), followed by stomatal closure stress two to four weeks later (Figure 5). Under ambient temperatures and drought conditions, time to mortality from water stress differed significantly among species (analysis of variance *F*-test, $F_{4,94} = 103.1$, $p < 0.0001$; post-hoc Tukey HSD test, Table 5b, Figure 6). Following the water stress inflection point, *Pinus ponderosa* juveniles died most quickly ($\bar{y}$ = 6.5 weeks, SD = 1.77, *n* = 20), followed by *Pinus edulis* ($\bar{y}$ = 10.5 weeks, SD = 2.89, *n* = 19), *Picea engelmannii* ($\bar{y}$ = 11.7 weeks, SD = 1.41, *n* = 20), *Pseudotsuga menziesii* ($\bar{y}$ = 11.9 weeks, SD = 1.45, *n* = 20), and *Pinus flexilis* ($\bar{y}$ = 19.0 weeks, SD = 2.15, *n* = 20).

Under ambient temperatures and drought conditions, the time to mortality from stomatal closure stress also differed significantly among species (analysis of variance *F*-test, $F_{4,45} = 27.1$, $p < 0.0001$; post-hoc Tukey HSD test, Table 5c, Figure 7). *Pinus ponderosa* tree juveniles died most quickly ($\bar{y}$ = 5.0 weeks, SD = 1.83, *n* = 10), followed by *Pinus edulis* ($\bar{y}$ = 6.8 weeks, SD = 2.44, *n* = 10), *Picea engelmannii* ($\bar{y}$ = 7.0 weeks, SD = 1.94, *n* = 10), *Pseudotsuga menziesii* ($\bar{y}$ = 8.1 weeks, SD = 1.29, *n* = 10), and finally *Pinus flexilis* ($\bar{y}$ = 14.2 weeks, SD = 2.86, *n* = 10).

Across all levels of analysis—with and without adjusting to time of onset of stress – *Pinus Ponderosa* died significantly earlier and *Pinus flexilis* died significantly later than most other species (Table 5a-c). These contrasts did not change when analyzing species under the drought-heatwave treatment (Table 5a-c). Adjusting the time to mortality by stress points or stomatal closure did not change the order that species died. The species most vulnerable to drought was *Pinus ponderosa*, followed by *Pinus edulis*, *Picea engelmannii*, *Pseudotsuga menziesii*, and *Pinus flexilis*.

## Discussion

### *Species Differences in Juvenile Vulnerability to Drought*

The ability of juvenile trees to survive prolonged drought is a key determinant of forest regeneration capacity, informing future forest composition under extreme climate conditions and following severe disturbances (Stevens-Rumann et al., 2022). We implemented an experimental drought which lasted until all individuals had died, exploring the bounds of how long juvenile trees can persist under conditions of extended drought compounded by a heatwave. Our study indicates substantial differences in species vulnerabilities to drought at the juvenile life stage. The length of a lethal drought for lower elevation species was short: 11 weeks for juvenile *Pinus ponderosa* and 14 weeks for *Pinus edulis*. Higher elevation species did not reach mortality until much later: 20 weeks for *Pseudotsuga menziesii* and *Picea engelmannii*, and 30 weeks for *Pinus flexilis*.

Droughts of this duration are within the range of climatic episodes that have occurred in recent decades (e.g. late 2001-2002; Breshears et al. 2009), and that are projected for an altered-climate future. Under historical and current climate conditions, a 30-week drought strong enough to induce widespread mortality of *Pinus flexilis* might occur once in century (Adams et al., 2009; Fig 3). In contrast, a 20-week drought would be twice as likely, and a 10-week drought strong enough to induce *Pinus ponderosa* mortality would be twenty times more likely (Adams et al., 2009; Fig 3). Thus, species such as *Pinus ponderosa* may be more vulnerable to drought-induced mortality due to the greater likelihood of shorter droughts, especially at the juvenile life stage. Notably, the drought conditions leading up to the die-off event documented in our study area for adult trees in 2002 (Breshears et al. 2005) had anomalously low precipitation for most of all 52 weeks of that year (Breshears et al. 2009; Fig A1), highlighting the potential for a protracted drought as in our experiment. Droughts within a single year may additionally be compounded by interannual drought such as in the southwest U.S., which is currently in a 20-year megadrought matching both the length and duration of the worst drought in the past 450 years (Williams et al., 2022).

### *Species Differences in Juvenile Heatwave Vulnerability*

Heatwave impacts on juvenile trees in our study were relatively minor, yet consistent. Across all species, the average time to mortality was faster among individuals with heatwave exposure. For two high elevation species – *Pinus flexilis* and *Pseudotsuga menziesii* – this difference was statistically significant, accelerating average time to mortality by two to three weeks. Despite observations of heatwaves having initiated large tree mortality events (Ruthrof et al., 2018), crown dieback of trees (Matusick et al., 2018), and reduced productivity (Ciais et al., 2005), this study found that the impact of a heatwave was small relative to the duration of the drought, perhaps because some individuals were already experiencing physiological stress from drought at that point. We initiated our heatwave at week seven during the dry-down process; at this time point, only *Pinus ponderosa* had progressed to stomatal closure, and the three higher elevation species had not reached the soil moisture inflection point. Thus, our results suggest that the timing and duration of a heatwave could determine its effect on time to mortality among species (Breshears et al. 2021). We found that a heatwave alone did not trigger mortality in watered juveniles. Hotter temperatures during drought pose a triple threat to plants: amplification of atmospheric drought (or increased vapor pressure deficit), intensified soil drought, and direct effects of heat stress (Hammond et al., 2022). Other studies report that heatwaves do not directly damage leaf tissue, but instead intensify drought conditions (De Boeck et al., 2010; Salomón et al., 2022); the relatively small impacts in time to mortality for juveniles exposed to heatwaves could be due to this factor as well as associated physiological impacts.

### *Concurrent Influences of Physiology, Ecohydrology, and Site Temperature*

Differences in time to mortality among species at the juvenile stage are a complex emergent response resulting from three key factors: (1) species-specific vulnerability to embolism during drought, (2) the associated ecohydrological response (for example, how that climate and the juvenile canopy structure affect soil evaporation), and (3) the climate conditions to which juvenile trees were exposed.

Embolism in response to protracted drought is a key driver of plant mortality (Choat et al. 2012; Adams et al. 2017; McDowell et al. 2022). Drought-stressed plants may undergo cavitation in their xylem cells, disrupting their water transport system (Choat et al., 2018). A common metric of drought tolerance is $\Psi_{50}$, the water potential of a plant when 50% of its water transport system has been disrupted by cavitation (Choat et al., 2012). Species with a more negative $\Psi_{50}$ value can tolerate more extreme drought conditions before losing hydraulic function. Research on $\Psi_{50}$ values suggests that, among our study species, *Pinus ponderosa* would have the greatest vulnerability to drought, followed by *Pseudotsuga menziesii*, *Pinus flexilis*, *Pinus edulis*, and finally *Picea engelmannii* (Choat et al., 2012; Domec and Gartner, 2001). In our study, *Pinus ponderosa* had the shortest time to mortality, consistent with this prediction. However, time to mortality among the other four species did not match this expected embolism order, even when we corrected our time to mortality based on stress metrics. A potentially co-occurring driver of mortality among plants is carbon starvation via stomatal closure (McDowell et al., 2008; Peltier et al., 2021). In this study, stomatal closure followed water stress points by two to four weeks across all species. The time from stomatal closure to mortality, on the other hand, varied widely across species. While most species reached mortality five to eight weeks following stomatal closure, *Pinus flexilis* survived for thirteen weeks. These differences in time to mortality possibly could be attributed to higher tolerance to carbon limitation or even greater carbon reserves to withstand longer periods of stomatal closure, although our study was not designed to elucidate this mechanism. The early mortality in *Pinus ponderosa* is consistent with mechanisms of both embolism and carbon starvation, but leaves open questions about the mechanisms of drought and temperature vulnerability in the other species at the juvenile stage.

Ecohydrological factors – how plant structure interacts with environmental conditions to influence water availability – may help to elucidate the role of evapotranspiration in this study (D'Odorico et al., 2010; Rodriguez-Iturbe, 2000). More open tree canopy architecture can allow greater evapotranspiration and water loss, while closed canopy structures can shade soil and retain moisture (Royer et al., 2012). In this study, *Pinus flexilis* was observed to have more compact needles with branches concentrated near the soil, which may have led to greater water retention. Even after soil moisture became more limiting, lower evaporation rates may have extended the time *Pinus flexilis* was able to survive.

Current species elevational distribution, represented in this study with corresponding temperature ranges, substantially influenced differing mortality rates among species. We expected that lower elevation species growing in warmer and drier environments would have more adaptations to withstand drought stress. Instead, we found that warm ambient temperatures led to high evapotranspiration rates and water loss, followed by more rapid species death. Cooler ambient temperatures of higher elevation species, conversely, acted as a buffer against drought conditions presumably by slowing the loss of water through evaporation; longer droughts were necessary before higher elevation species would reach water stress, perhaps overriding expected differences in drought tolerance due to tree physiology.

All three interacting factors of species physiology, ecohydrological influences, and temperatures effects could influence our experimental results. Nonetheless, the outcomes of this study indicate the potential consequences of prolonged drought and heatwave exposure at the juvenile state across species, adding to our overall understanding of these species' drought tolerances at critical demographic life stages.

### *Limitations and Future Work*

We acknowledge several limitations in this preliminary study. First, we used growth chambers to implement a controlled heatwave event and normalize drought stress across species to compare stress tolerance, which would be difficult to implement in a replicated field setting. Second, as is typical with growth chamber experiments, individuals within each chamber may be spatially correlated in their responses, and results can be difficult to translate to the landscape scale. Third, conductance measurements are sensitive to fluctuations in humidity and temperature; to maintain measurement accuracy, we calibrated the porometer weekly. Fourth, ecohydrological influences with landscape topography, microclimate, and the broader plant community can attenuate climate drivers of heat and drought, influencing water stress among species. Fifth, as is often the case in reforestation efforts, plant material did not originate from the specific study region, and regional species adaptations were therefore not reflected in this study. This is particularly important when making predictions for how species might respond across elevational gradients, as recent studies have suggested that epigenetic responses (heritable traits in juveniles in response to stresses experienced by the parent organism) may help mitigate localized stress to drought heat stress (Amaral et al., 2020; Backs and Ashley, 2021; Carneros et al., 2017). Overall, we employed temperature conditions within the typical elevation range for ecologically co-occurring species the Jemez Mountains, and this study design was appropriate for imposing consistent environmental conditions across species.

Potential limitations in our experimental design suggest promising future lines of research. More mechanistic methods to complement our insights into drought tolerance would require a larger sample size to allow for weekly destructive sampling (e.g. of biomass, plant water potential and non-structural carbohydrates) or rewatering plants at different time intervals to estimate when plants cannot recover (e.g. Hammond et al., 2019). Estimates of plant death and percent brown are consistent with other plant mortality studies as relative measures, yet these are still whole-plant subjective measurements with coarse definitions. We mitigated subjectivity by having one technician consistently evaluating tree mortality metrics, and by developing and testing an objective, quantifiable, and repeatable method of image analysis. Multispectral or hyperspectral image data include a wider and more finely resolved array of wavelengths beyond what would be detected by ocular estimates such as near infrared wavelengths that are longer than the visible wavelengths.

To uncover the impacts of heatwave at various stress points, future growth chamber studies could adjust heatwave timing, duration (days), and intensity (degrees of increase) after the onset of drought. A differently parameterized heatwave experiment (e.g. suggestions in Breshears et al. 2021) would help to explore the dimensions of heatwave impacts. Our drought experimental framework could be expanded to include re-watering of trees following varying intervals of drought, to examine the recovery potential of individuals. These results could be complemented with further studies of the effects of warming baseline temperatures on species vulnerability (e.g. Adams et al. 2009; Adams et al. 2017) for a more complete picture of future forest change.

### *Ecological and Management Implications*

Drought and temperature regimes, and widespread disturbances, will almost certainly have a prominent role in shaping future species distributions. Landscape-scale droughts and periodic heatwaves are likely to become persistent climate factors in the Southwest (Guirguis et al., 2018; Williams et al., 2020). The backdrop of drought, even within the context of species-specific climatic adaptations, will be a determining factor in the survival of tree species to a rapidly changing climate. In this dynamic environment, young trees represent a critical demographic stage allowing species ranges to shift, especially toward the leading edge of the species distribution (Talluto et al. 2017; Parks et al. 2019). Young trees are also the prevailing mode of post-fire restoration, where naturally occurring seed dispersal is either limited or absent (Shive et al. 2018; North et al. 2019; Stevens-Rumann et al. 2019).

This study expands the scope of forest recovery beyond initial seedling establishment following disturbance, to include persistence against subsequent climate pressures during early tree development. Our results uncover substantial species-specific responses to drought and heat at the juvenile growth stage. When normalizing species to different levels of stress, *Pinus flexilis* survived three times longer than *Pinus ponderosa* at the juvenile growth stage, while *Pinus edulis*, *Picea engelmannii*, and *Pseudotsuga menziesii* had comparable tolerance with intermediate survival rates. We also saw a pronounced temperature effect, where warmer baseline temperatures allow drought conditions to be realized more quickly.

The relatively high vulnerability of *Pinus ponderosa* to drought seems surprising given its dominance in dry landscapes across the Southwest (Oliver and Russell, 1990). *Pinus ponderosa* is highly adapted to dry, fire-frequent landscapes, with traits such as thick bark and elevated crowns to avoid fire damage (Falk et al., 2022). As a mature tree, *Pinus ponderosa* can survive low intensity fire disturbance, but juveniles are considerably less fire resistant (Partelli-Feltrin et al., 2020). Juvenile regeneration in the species is episodic and highly dependent on climate (Mast et al., 1999; White, 1985);  several years of favorable climate are needed to support juvenile survival and growth (Kemp et al., 2019). Although mature *Pinus ponderosa* may be favored at lower elevations due to its fire adaptations, juveniles facing climate extremes may be vulnerable in the warm-dry tails of their climatic range. In contrast, *Pinus flexilis* have a relatively small abundance in the Jemez Mountains despite their drought tolerance (Muldavin and Tonne, 2003). *Pinus flexilis* is concentrated on rocky dry sites in cool environments where they hold a competitive advantage over other conifers, including the closely related species *Pinus strobiformis* Engelmann (southwestern white pine) (Menon et al., 2021). They can be found scattered throughout the mixed conifer zone, but are successionally replaced by spruce and fir species on most sites (Rebertus et al., 1991). As this study suggests, *Pinus flexilis* may gain a competitive advantage in sites where forest species must contend with lengthening droughts.

Natural and managed forest regeneration is dependent on the ability of tree juveniles to survive expected climate anomalies. Many forest and woodland ecosystems in the Southwest are forecast to be highly vulnerable to vegetation conversion, based on species distributions and shifting climate envelope models (Triepke et al., 2019). Strategic tree planting, especially in the context of prolonged drought, is an active management technique that can mitigate regeneration failure (Field et al., 2020). Planting in clusters where climate conditions are most suitable (refugia; e.g. McDowell et al., 2019) can facilitate regeneration among disturbed landscapes (Stevens et al., 2021). The juvenile age class, as examined in this study, is especially relevant to managed reforestation strategies (Landis et al., 2010).

Our study employed juvenile trees acquired from nurseries, and our results can thus inform managers concerned with potential success of outplanting under emerging climate conditions. This demographic stage is key to implementing mechanistic models of forest ecological resilience (Falk 2017; Falk et al. 2022). In turn, ecological resilience is the foundation for emerging management and adaptation paradigms, including the Resist-Resilience-Transition (Peterson St-Laurant et al. 2021) or Resist-Accept-Direct (RAD; Thompson et al. 2018) management frameworks. Resisting change through recovery would be focused on planting a species according to its historic distribution, which may require ongoing active management to resist persistent drought conditions. On the other hand, planting species at higher elevations with cooler temperatures would represent a transition approach, facilitating upward migration of species (Brusca et al., 2013; Parks et al., 2019). Other transition approaches might include planting more climatically-plastic species such as *Pinus flexilis*, which are not currently dominant on the landscape but may become more widespread in the future. Adaptive management will be especially important in the face of uncertain climate futures (Jackson, 2021).

In conclusion, our incorporation of drought and temperature tolerance at the juvenile demographic stage fills a key information gap regarding potential species persistence, recovery, and range shifts over time. Future management actions and planting strategies could consider these experimental outcomes to anticipate landscape-level climate impacts on juvenile tree survival as the key to species adaption in a rapidly changing world.

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# FIGURES

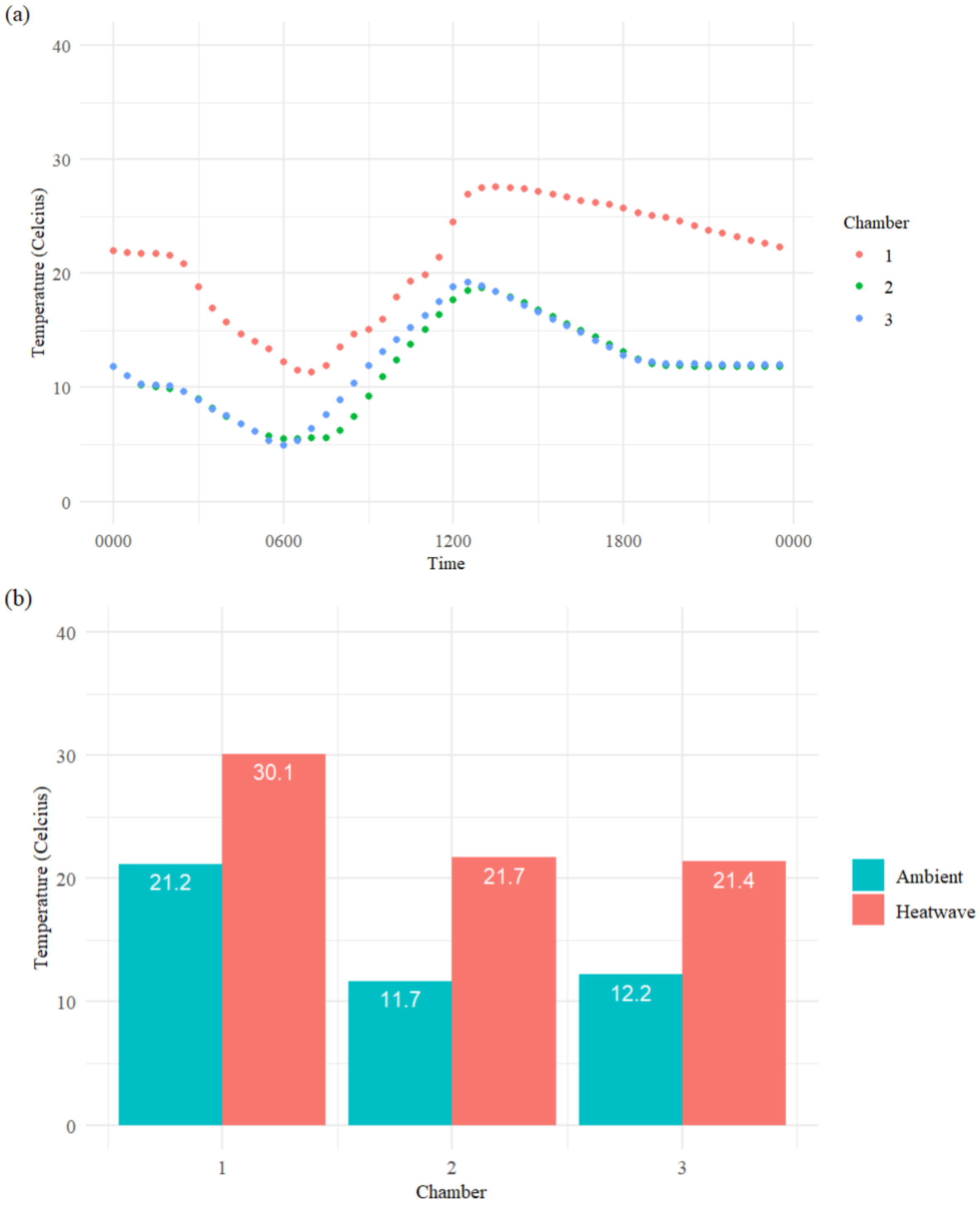

**FIGURE 1 |** Temperature Settings of Growth Chambers.
Graphs show diurnal temperature fluctuations in the growth chambers (a) and average temperatures for ambient and heatwave treatments (b).

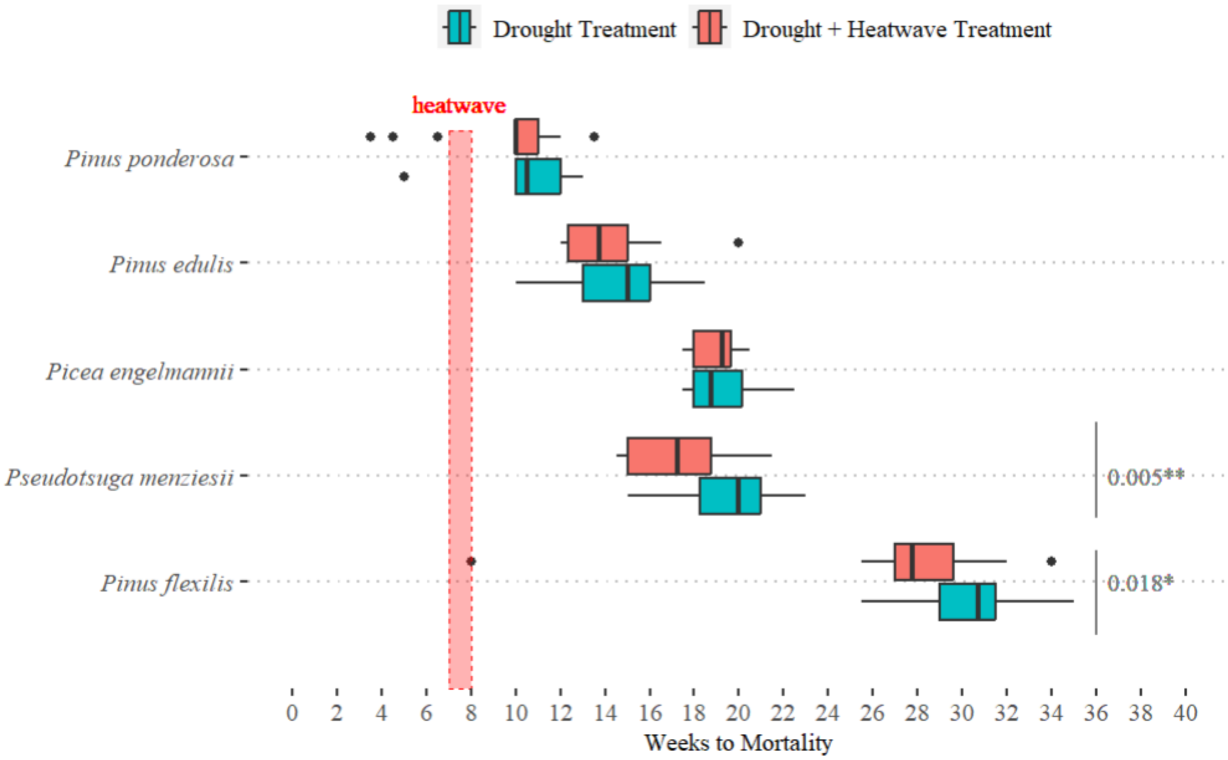

**FIGURE 2 |** Heatwave Differences of Droughted Juveniles.
Half the droughted individuals (n = 20 per species) were exposed to a week-long heatwave (indicated by the vertical red box). Boxplots show median time to mortality (rather than the mean). Grey bars on the right-hand side show p-values of species which are significantly different in their mean time to mortality (two-sample t-test, $p < 0.05$).

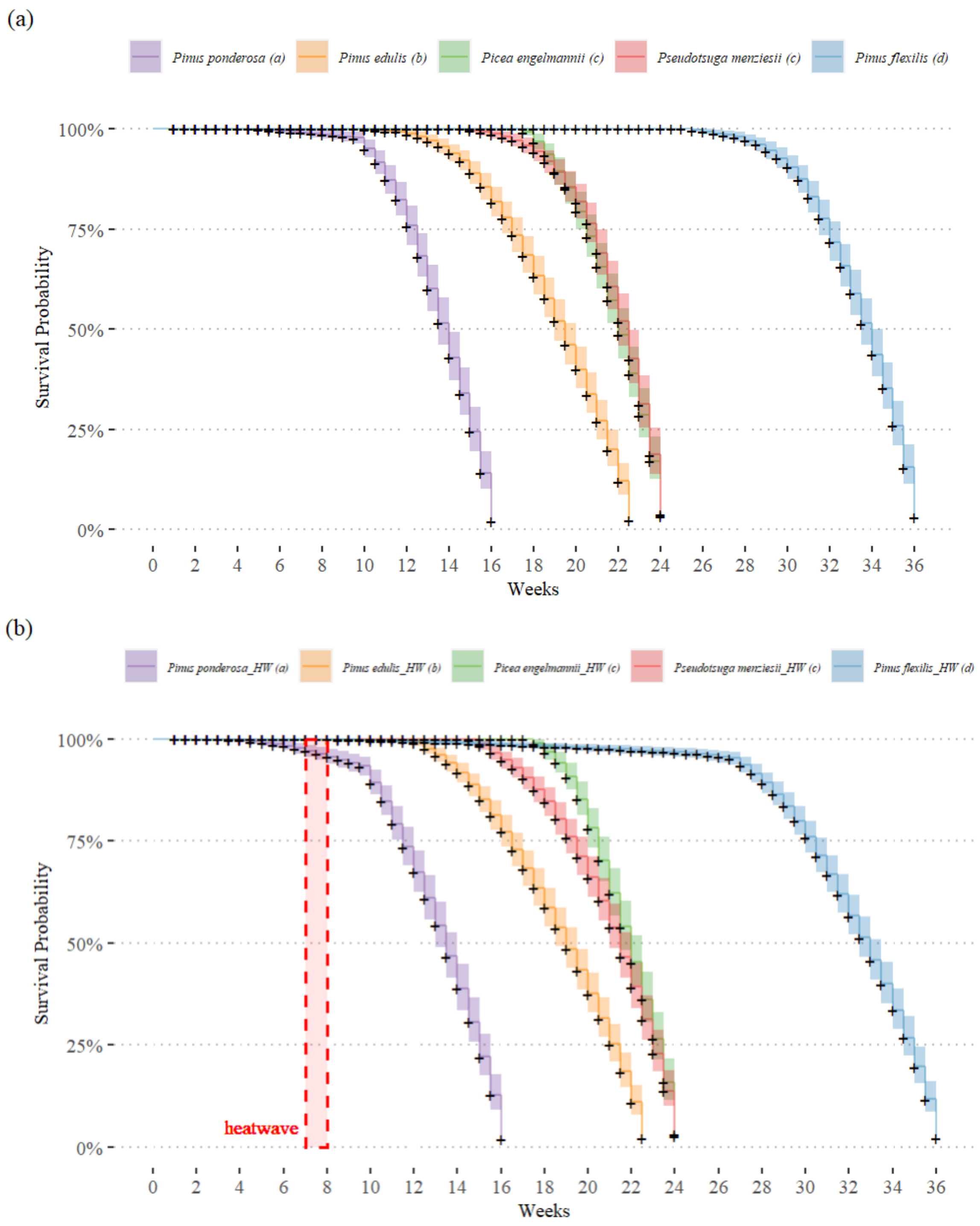

**FIGURE 3 |** Kaplan Meier Survival Curve of Juvenile Survival Probability under Drought. Curves shows the survival probability of each species under ambient (a) and heatwave (b) temperature treatments. Weeks show time since the start of the experiment, adjusted to account for staggered start times. Letters in the legend (a, b, c, d) show species which are significantly different (post-hoc Tukey HSD test, $p < 0.05$).

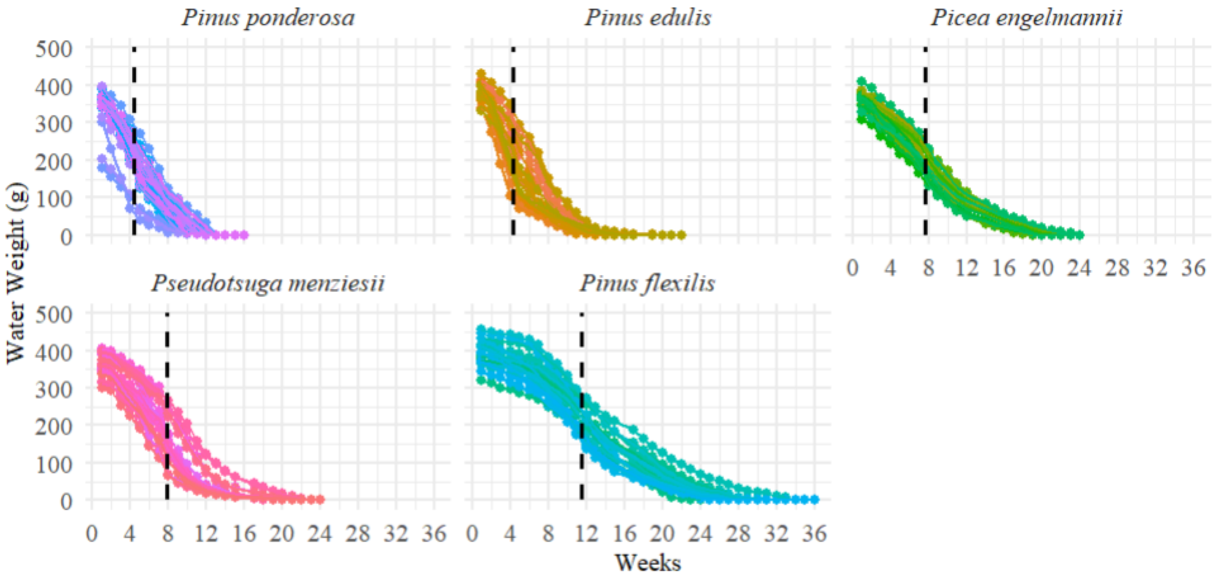

**FIGURE 4 |** Water Weight of Juveniles under Droughted and Ambient Treatments. Curves were calculated using individual weight data (n = 20 per species). Black dotted lines show the average inflection point among all curves to show where concavity changes from concave up to concave down, reflecting the time when water availability transitioned from a non-limiting to a limiting resource.

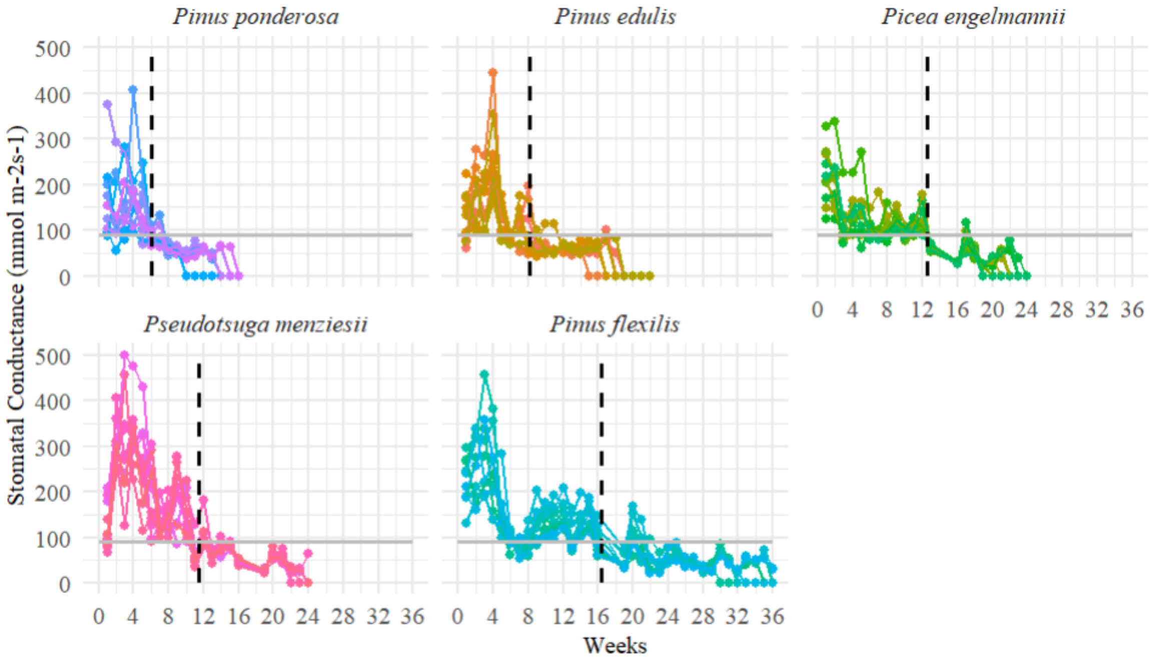

**FIGURE 5 |** Stomatal Conductance of Juveniles under Droughted and Ambient Treatments. The black dotted line shows the average time of permanent stomatal closure (n = 10 per species), when measurements were consistently at or below a minimum value of 90 mmol m-2s-1 (solid gray horizonal line).

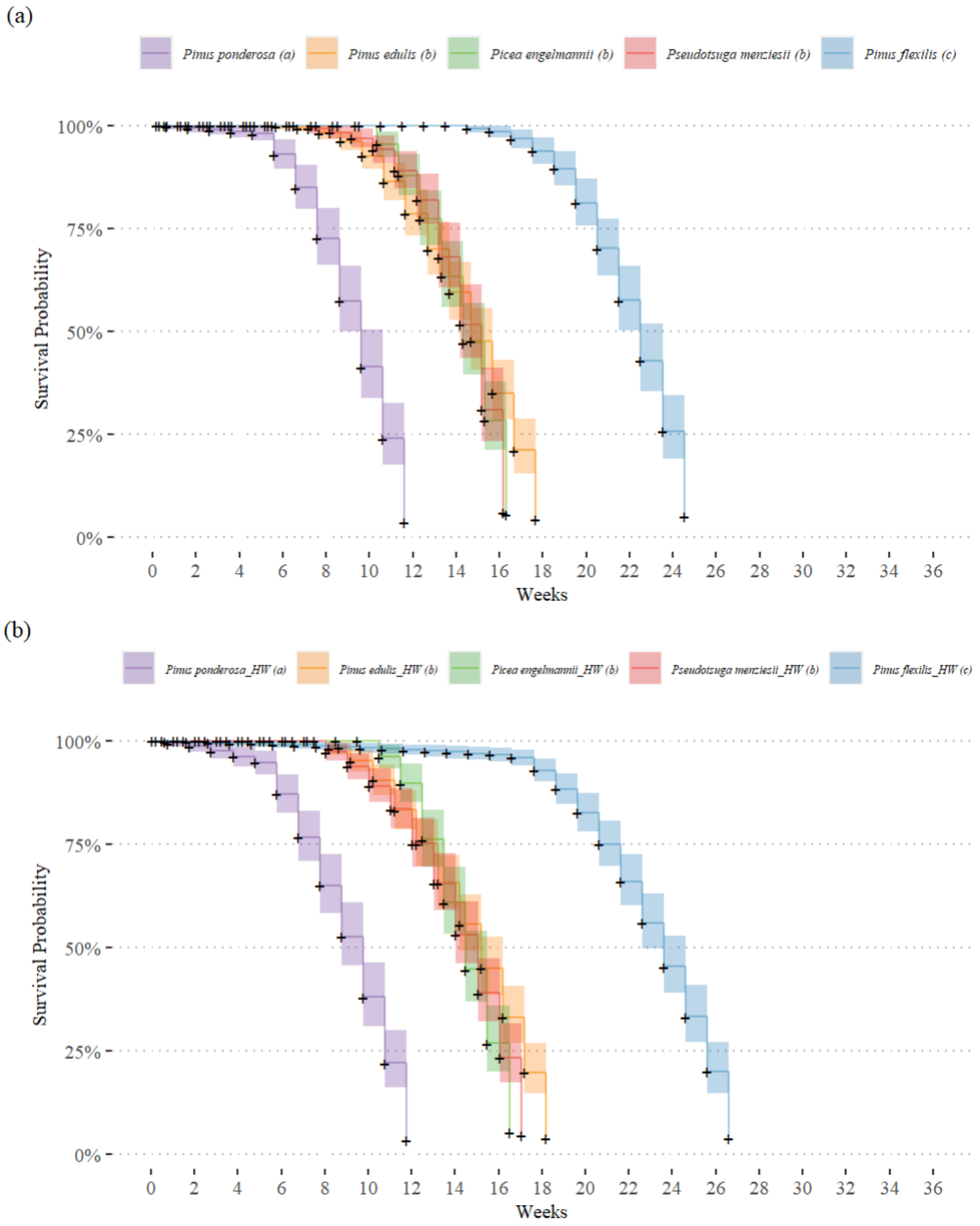

**FIGURE 6 |** Kaplan Meier Survival Curve of Juvenile Survival Probability under Drought, Adjusted by Water Stress.
Curves shows the survival probability of each species under ambient (a) and heatwave (b) temperature treatments. Weeks show time since water stress for each individual (*n* = 20 per species). Letters in the legend (a, b, c) show species which are significantly different (post-hoc Tukey HSD test, $p < 0.05$).

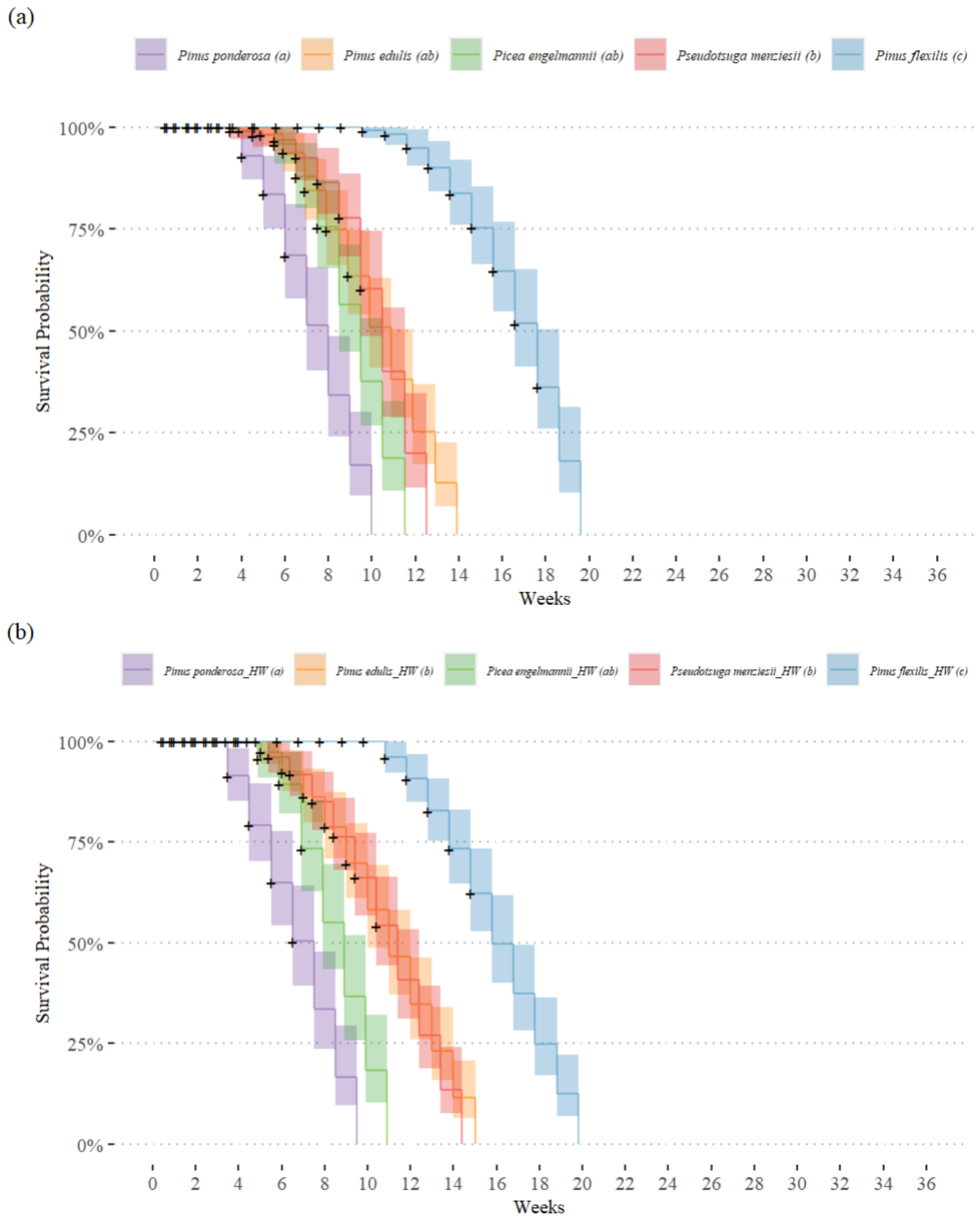

**FIGURE 7 |** Kaplan Meier Survival Curve of Juvenile Survival Probability under Drought, Adjusted by Permanent Stomatal Closure Stress.
Curves shows the survival probability of each species under ambient (a) and heatwave (b) temperature treatments. Weeks show time since permanent stomatal closure stress for each measured individual (*n* = 10 per species). Letters in the legend (a, b, c) show species which are significantly different (post-hoc Tukey HSD test, $p < 0.05$).

# TABLES

**TABLE 1 |** June temperature average and diurnal ranges for each species group, used for growth chamber settings.

| **Species** | **Average Ambient Temperature and Diurnal Range (°C)** | **Average Heatwave Temperature and Diurnal Range (°C)** |
|---|---|---|
| *Pinus edulis*<br>*Pinus ponderosa* | 21.2<br>(Diurnal Range = 11.2 to 27.7) | 30.1<br>(Diurnal Range = 18.7 to 36.3) |
| *Pinus flexilis*<br>*Pseudostuga menziesii* | 11.7<br>(Diurnal Range = 5.4 to 18.9) | 21.7<br>(Diurnal Range = 13.6 to 27.5) |
| *Picea engelmanni* | 12.2<br>(Diurnal Range = 4.8 to 19.4) | 21.4<br>(Diurnal Range = 13.8 to 29.1) |

**TABLE 2 |** Heatwave parameters in this study compared to similar previous studies and to a global review of current heatwave averages.

| **Citation** | **Location** | **Duration (days)** | **°C Increase** | **Ambient Average** | **Heatwave Average** |
|---|---|---|---|---|---|
| This Study | Arizona (low elev.) | **7** | **9** | 21 | 30 |
| This Study | Arizona (high elev.) | **7** | **9 to 10** | 12 | 21.5 |
| Marchin et al 2022 | Australia | **6** | **7** | 28 | 35 |
| Notarnicola et al 2021 | Australia (historic) | **5** | **5** | 24 | 29 |
| Notarnicola et al 2021 | Australia (future +5 °C) | **5** | **5** | 29 | 34 |

**TABLE 3 |** Summary of sample size, age, height, basal diameter, and dry biomass of juvenile trees, by species.

| **Species** | ***n*** | **Median Age (whorls count)** | **Average Height (mm)** | **Average Basal Diameter (mm)** | **Average Dry Biomass (g)** |
|---|---|---|---|---|---|
| *Pinus edulis* | 49 | 4 ± 0.74 | 293 ± 89.8 | 6.09 ± 1.54 | 7.64 ± 4.13 |
| *Pinus ponderosa* | 50 | 4 ± 0.86 | 195 ± 62.0 | 6.92 ± 1.50 | 4.60 ± 2.24 |
| *Pinus flexilis* | 50 | 4 ± 1.05 | 136 ± 35.6 | 5.82 ± 1.05 | 3.58 ± 1.11 |
| *Pseudostuga menziesii* | 50 | 4 ± 1.03 | 394 ± 56.9 | 6.21 ± 0.80 | 7.23 ± 2.00 |
| *Picea engelmanni* | 50 | 4 ± 0.75 | 266 ± 39.2 | 5.89 ± 1.02 | 4.58 ± 1.23 |

**TABLE 4 |** Results from two-sample *t*-test of temperature effects (ambient and heatwave treatment groups) on species.

| Species | Heatwave | | Ambient | | Difference in Time to Mortality (Weeks) | *t*-value | one-sided *p*-value |
|---|---|---|---|---|---|---|---|
| | ***n*** | **Mean Time to Mortality (Weeks)** | ***n*** | **Mean Time to Mortality (Weeks)** | | | |
| *Pinus edulis* | 20 | 14.0 ± 2.06 | 19 | 14.6 ± 2.17 | -0.6 ± 1.2 | -0.89 | 0.188 |
| *Pinus ponderosa* | 20 | 9.7 ± 2.32 | 20 | 10.7 ± 1.71 | -1.0 ± 1.1 | -1.63 | 0.056 |
| *Pinus flexilis* | 20 | 27.6 ± 5.05 | 20 | 30.3 ± 2.39 | -2.7 ± 2.1 | -2.16 | 0.018* |
| *Pseudostuga menziesii* | 20 | 17.4 ± 2.39 | 20 | 19.4 ± 2.31 | -2.0 ± 1.3 | -2.69 | 0.005** |
| *Picea engelmanni* | 20 | 18.9 ± 1.02 | 20 | 19.2 ± 1.51 | -0.3 ± 0.7 | -0.68 | 0.252 |

**TABLE 5a |** Results from post-hoc Tukey HSD test, performed on original data (not stress normalized). Results show separate analyses for ambient and heatwave treatments. Highlighted cells indicate species which are significantly different ($p < 0.05$). Species comparison codes are defined as: PIPO = *Pinus ponderosa*; PIED = *Pinus edulis*; PIFL = *Pinus flexilis*; PIEN = *Picea engelmanni*; PSME = *Pseudostuga menziesii*

| **Species Differences: post-hoc Tukey HSD test** | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Ambient** | | | | | **Heatwave** | | | | |
| **Species** | **Difference (Weeks)** | **Lower CI (Weeks)** | **Upper CI (Weeks)** | ***p*-value** | **Species** | **Difference (Weeks)** | **Lower CI (Weeks)** | **Upper CI (Weeks)** | ***p*-value** |
| PIEN-PIED | 4.6 | 2.8 | 6.4 | $4.71 \times 10^{-9}$ | PIEN-PIED | 4.9 | 2.4 | 7.4 | $5.78 \times 10^{-6}$ |
| PIFL-PIED | 15.7 | 13.9 | 17.5 | $4.84 \times 10^{-10}$ | PIFL-PIED | 13.6 | 11.0 | 16.1 | $4.63 \times 10^{-10}$ |
| PIPO-PIED | -3.9 | -5.7 | -2.1 | $4.27 \times 10^{-7}$ | PIPO-PIED | -4.4 | -6.9 | -1.8 | $6.80 \times 10^{-5}$ |
| PSME-PIED | 4.8 | 3.0 | 6.6 | $1.18 \times 10^{-9}$ | PSME-PIED | 3.4 | 0.9 | 6.0 | $2.80 \times 10^{-3}$ |
| PIFL-PIEN | 11.1 | 9.3 | 12.9 | $4.84 \times 10^{-10}$ | PIFL-PIEN | 8.7 | 6.1 | 11.2 | $4.64 \times 10^{-10}$ |
| PIPO-PIEN | -8.5 | -10.3 | -6.7 | $4.84 \times 10^{-10}$ | PIPO-PIEN | -9.3 | -11.8 | -6.7 | $4.64 \times 10^{-10}$ |
| PSME-PIEN | 0.3 | -1.6 | 2.1 | 0.9950 | PSME-PIEN | -1.5 | -4.0 | 1.1 | 0.4931 |
| PIPO-PIFL | -19.6 | -21.4 | -17.8 | $4.84 \times 10^{-10}$ | PIPO-PIFL | -17.9 | -20.5 | -15.4 | $4.63 \times 10^{-10}$ |
| PSME-PIFL | -10.9 | -12.7 | -9.1 | $4.84 \times 10^{-10}$ | PSME-PIFL | -10.2 | -12.7 | -7.6 | $4.63 \times 10^{-10}$ |
| PSME-PIPO | 8.7 | 6.9 | 10.5 | $4.84 \times 10^{-10}$ | PSME-PIPO | 7.8 | 5.2 | 10.3 | $4.63 \times 10^{-10}$ |
| Species (all) | | | | $< 2 \times 10^{-16}$ | Species (all) | | | | $< 2 \times 10^{-16}$ |

**TABLE 5b |** Results from post-hoc Tukey HSD test, performed on data which were normalized for water stress. Results show separate analyses for ambient and heatwave treatments. Highlighted cells indicate species which are significantly different ($p < 0.05$). Species comparison codes are defined as: PIPO = *Pinus ponderosa*; PIED = *Pinus edulis*; PIFL = *Pinus flexilis*; PIEN = *Picea engelmanni*; PSME = *Pseudostuga menziesii*

| **Species Differences, Normalized for Water Stress: post-hoc Tukey HSD test** | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Ambient** | | | | | **Heatwave** | | | | |
| **Species** | **Difference (Weeks)** | **Lower CI (Weeks)** | **Upper CI (Weeks)** | ***p*-value** | **Species** | **Difference (Weeks)** | **Lower CI (Weeks)** | **Upper CI (Weeks)** | ***p*-value** |
| PIEN-PIED | 1.3 | -0.5 | 3.0 | 0.2923 | PIEN-PIED | 1.2 | -1.6 | 3.9 | 0.7638 |
| PIFL-PIED | 8.6 | 6.8 | 10.3 | $4.84 \times 10^{-10}$ | PIFL-PIED | 7.9 | 5.2 | 10.7 | $4.97 \times 10^{-10}$ |
| PIPO-PIED | -4.0 | -5.8 | -2.2 | $1.17 \times 10^{-7}$ | PIPO-PIED | -4.9 | -7.7 | -2.2 | $3.01 \times 10^{-5}$ |
| PSME-PIED | 1.5 | -0.3 | 3.2 | 0.1596 | PSME-PIED | 0.2 | -2.5 | 3.0 | 0.9993 |
| PIFL-PIEN | 7.3 | 5.5 | 9.1 | $4.84 \times 10^{-10}$ | PIFL-PIEN | 6.8 | 4.0 | 9.5 | $9.78 \times 10^{-9}$ |
| PIPO-PIEN | -5.3 | -7.0 | -3.5 | $4.90 \times 10^{-10}$ | PIPO-PIEN | -6.1 | -8.9 | -3.3 | $1.92 \times 10^{-7}$ |
| PSME-PIEN | 0.2 | -1.6 | 2.0 | 0.9976 | PSME-PIEN | -0.9 | -3.7 | 1.8 | 0.8799 |
| PIPO-PIFL | -12.6 | -14.3 | -10.8 | $4.84 \times 10^{-10}$ | PIPO-PIFL | -12.8 | -15.6 | -10.1 | $4.63 \times 10^{-10}$ |
| PSME-PIFL | -7.1 | -8.9 | -5.3 | $4.84 \times 10^{-10}$ | PSME-PIFL | -7.7 | -10.4 | -4.9 | $5.70 \times 10^{-10}$ |
| PSME-PIPO | 5.5 | 3.7 | 7.2 | $4.85 \times 10^{-10}$ | PSME-PIPO | 5.1 | 2.4 | 7.9 | $1.14 \times 10^{-5}$ |
| Species (all) | | | | $< 2 \times 10^{-16}$ | Species (all) | | | | $< 2 \times 10^{-16}$ |

**TABLE 5c |** Results from post-hoc Tukey HSD test, performed on data which were normalized for permanent stomatal closure stress. Results show separate analyses for ambient and heatwave treatments. Highlighted cells indicate species which are significantly different ($p < 0.05$). Species comparison codes are defined as: PIPO = *Pinus ponderosa*; PIED = *Pinus edulis*; PIFL = *Pinus flexilis*; PIEN = *Picea engelmanni*; PSME = *Pseudostuga menziesii*

| **Species Differences, Normalized for Permanent Stomatal Closure Stress: post-hoc Tukey HSD test** | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Ambient** | | | | | **Heatwave** | | | | |
| **Species** | **Difference (Weeks)** | **Lower CI (Weeks)** | **Upper CI (Weeks)** | ***p*-value** | **Species** | **Difference (Weeks)** | **Lower CI (Weeks)** | **Upper CI (Weeks)** | ***p*-value** |
| PIEN-PIED | 0.2 | -2.5 | 2.9 | 0.9996 | PIEN-PIED | -0.8 | -3.2 | 1.6 | 0.8761 |
| PIFL-PIED | 7.4 | 4.7 | 10.1 | $8.38 \times 10^{-9}$ | PIFL-PIED | 5.4 | 3.0 | 7.8 | $7.66 \times 10^{-7}$ |
| PIPO-PIED | -1.8 | -4.5 | 0.9 | 0.3423 | PIPO-PIED | -2.8 | -5.2 | -0.4 | 0.014658 |
| PSME-PIED | 1.3 | -1.4 | 4.0 | 0.6568 | PSME-PIED | 0.5 | -1.9 | 2.9 | 0.9755 |
| PIFL-PIEN | 7.2 | 4.5 | 9.9 | $1.70 \times 10^{-8}$ | PIFL-PIEN | 6.2 | 3.8 | 8.6 | $3.02 \times 10^{-8}$ |
| PIPO-PIEN | -2.0 | -4.7 | 0.7 | 0.2423 | PIPO-PIEN | -2.0 | -4.4 | 0.4 | 0.1420 |
| PSME-PIEN | 1.1 | -1.6 | 3.8 | 0.7795 | PSME-PIEN | 1.3 | -1.1 | 3.7 | 0.5416 |
| PIPO-PIFL | -9.2 | -11.9 | -6.5 | $1.78 \times 10^{-11}$ | PIPO-PIFL | -8.2 | -10.6 | -5.8 | $1.26 \times 10^{-11}$ |
| PSME-PIFL | -6.1 | -8.8 | -3.4 | $8.49 \times 10^{-7}$ | PSME-PIFL | -4.9 | -7.3 | -2.5 | $5.76 \times 10^{-6}$ |
| PSME-PIPO | 3.1 | 0.4 | 5.8 | 0.018236 | PSME-PIPO | 3.3 | 0.9 | 5.7 | $2.70 \times 10^{-3}$ |
| Species (all) | | | | $1.8 \times 10^{-11}$ | Species (all) | | | | $3.5 \times 10^{-11}$ |