

Live fast, die young: Climate shifts may favor Great Basin bristlecone pine or limber pine in sub-alpine forest establishment

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ABSTRACT

As a result of climatic warming, tree species ranges are generally expected to move upslope in elevation. Although this upward range migration is likely determined principally by temperature, other factors such as habitat and soil moisture availability contribute to a species' ability to establish in new areas. Throughout the montane ecosystems of the western US, effective drying is predicted, resulting from increasing temperatures and potentially reduced precipitation. The tree species that can better establish in these future high-elevation forests will likely expand their ranges while potentially excluding other species. Using a greenhouse experiment, we compared the response of limber pine and Great Basin bristlecone pine, the two dominant Great Basin sub-alpine species, to various levels of drought at different stages during their establishment. We found that during the first year of establishment, limber pine had greater diameter growth but lower height growth than bristlecone pine, while during the second year of establishment, limber pine had greater diameter and height growth rates across all treatments. During the post-germination period and in the second year of establishment, bristlecone pine seedlings had a higher survival rate than limber pine. During the first year of establishment there was no determinable difference in survival between the species. Limber pine displayed earlier mortality and lower survival under nearly all treatments across both first-and second-year periods. In general, an increase in drought severity corresponded to an overall earlier mortality onset as well as decreased survival in both species. However, in the first year of establishment under the no water treatment, both species showed later mortality than all other treatments, even having longer survival durations than a treatment with slightly more water. Limber pine seedlings effectively grew at higher rates than bristlecone pine seedlings, while dying younger. The different response of each species to drought stress during the establishment phase suggests an asymmetric competition under two possible climate change scenarios: a warmer, wetter future may favor limber pine, while a warmer, drier future may favor GB bristlecone pine. For the Great Basin's sub-alpine forest community, this foreshadows a more complex future change in tree demographics than simple upslope migration.

1. Introduction

As a result of climatic warming, species are generally expected to expand their range into higher elevations and latitudes (Hayhoe et al., 2004; Lenoir et al., 2008; Parmesan and Yohe, 2003). While such species migration are likely predominantly controlled by temperature, there are a variety of other factors that can also affect the dynamics of these shifts (Dobrowski and Parks, 2016). In addition to temperature limitations, soil moisture availability may be an important influence on a species' ability to establish outside of its current range, especially in mountain

systems (Kueppers et al., 2017; Moyes et al., 2015). In high-elevation montane ecosystems of the western US, future climate scenarios predict precipitation to decrease during the growing season, leading to lower soil moisture availability (Melack et al., 1997; Mensing et al., 2008; Rixen and Wipf, 2017). Even if mean annual precipitation remains constant, increasing temperatures and decreases in the amount of precipitation as snow are already leading to effective drying (Barnett et al., 2008; Millar et al., 2007a, 2007b). In addition, biotic interactions, such as inter-specific competition, facilitation, or differential species responses can affect how species ranges respond to climate change (Davis

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et al., 2020). The mechanisms of plant responses to these complex interacting factors will largely determine species migration dynamics.

High-elevation plant communities are especially sensitive to both the abiotic and biotic factors that determine species distributions, as high-elevation species generally have relatively narrow climatic niches coupled with limited microclimatic habitat availability (Debinski et al., 2000; Harte and Shaw, 1995; Smithers et al., 2019). For high elevation sub-alpine tree species, which are limited at their upper range edges by treeline, modern climatic modeling is able to accurately predict current species distributions (Körner and Paulsen, 2004; Randin et al., 2009). These models also project upward elevational shifts of treelines on the scale of several hundreds of meters by the end of the century (Grace et al., 2002; Kullman and Öberg, 2009). Although higher temperatures and a lengthening growing season have been generally well documented globally, treeline advance has not been universal (Harsch et al., 2009). Where treeline has advanced upslope, the advance has been more moderate than predicted by temperature increases (Harsch et al., 2009; Körner and Paulsen, 2004; Smithers et al., 2018). The lack of universal treeline advance illustrates the complex nature of local-scale interactions and the inability to attribute treeline advance solely to increasing temperatures (Harsch et al., 2009).

The ability of sub-alpine forest to expand upslope is largely dependent on the most vulnerable life stage of the tree species composing the stand (Máliš et al., 2016). While adult trees are generally limited at their upper range edge by cold temperatures, young trees, even at high elevations, can be exposed to very warm and dry conditions at the soil surface during the growing season (Smithers, 2017). Young trees experience vastly different micro-climates while having narrower environmental tolerances than mature trees, which have deeper root systems and are decoupled from soil surface high temperatures (Dobrowski et al., 2015; Zhu et al., 2012). Because of this, young trees respond differently to climate than adult trees (Smithers et al., 2018). Once established, sub-alpine conifers have high survival rates, however pre-establishment survival rates are low in comparison (Barber, 2013; Germino et al., 2002; Malanson et al., 2007). With treeline range expansion depending largely on juvenile establishment, understanding the survival mechanisms of sub-alpine trees during the establishment phase is essential to accurately predicting how tree species' distributions are shifting in response to the range of abiotic and biotic pressures they face.

Due to thin, coarse soils and high solar exposure, soils upslope of treeline are generally drier than soils under the sup-alpine forest canopy (Moyes et al., 2015). Also, due to limited establishment microsite availability, competition between migrating species upslope is highly likely. The relative responses of competing species to these limiting stressors will structure future species dynamics above current treeline. Through a combination of increased temperature and reductions in precipitation, soil moisture availability is predicted to be reduced (Harvey et al., 2016; Lazarus et al., 2018). This limited sub-terranean access to moisture is especially limiting to juvenile trees. Mature trees are generally less affected by drought and can better withstand drought stress (Padilla and Pugnaire, 2007). Tree species that are better able to survive drought in the earliest life stages are likely to have an advantage in establishing new upslope forests, and given limited microsite availability, could potentially exclude species less able to do so.

Limber pine seedlings do not appear to be limited by temperature upslope of treeline in the Rocky Mountains (Kueppers et al., 2017). Rather, they appear to be more strongly limited by water availability (Moyes et al., 2013). Recent research has also shown that limber pine has colonized areas above treeline in much greater numbers than has GB bristlecone pine (Millar et al., 2015; Smithers et al., 2018). The relative ability of these species to respond to drought stress, especially at their most vulnerable life stage, is critical to their ability to compete for the limited water projected within the Great Basin and will likely shape the future community structure across Great basin sub-alpine forests.

Competition between forest tree species is generally a function of growth rates. Faster growth rates and greater tree bole widths are

typically an indicator of higher fitness (Arendt, 1997; Lanner, 2002). Faster growing trees often monopolize space for light and water resources, reducing the fitness of other species. In addition, faster growing trees typically reach reproductive age earlier, leading to the reduction of generation times, and an ability to more quickly establish climate adapted populations (Bigler and Veblen, 2009). Compared with other conifers, growth rates of high-elevation trees tend to be relatively low due to the short, cool growing season associated with high-elevation forests (Coomes and Allen, 2007). In high elevation forests in dry climates, this slow growth rate may also be an adaptation for minimizing the risk of drought-induced hydraulic failure (Petit et al., 2011). Therefore, sub-alpine tree species are likely to have opposing selective pressures: to grow fast to outcompete other species for resources while also attempting to limit the risk of hydraulic failure caused by high growth rates.

This study examines the growth and survival of limber pine and GB bristlecone pine in an induced drought greenhouse experiment across three of the earliest life stages: post-emergence as well as in the first and second year of establishment. Specifically, we hypothesize that 1) an increase in drought stress will lead to a higher mortality rate and lower growth rates in both species, 2) due to increased stored resources, the later life-stage individuals will have higher survival rates than earlier life-stage individuals in response to drought, and 3) since it is generally found further downslope and on drier soil types, limber pine will have higher survival than GB bristlecone pine in drought conditions.

2. Materials and methods

2.1. Study region and species

In the Great Basin of the United States, a region of more than 200 individual mountain ranges between the California Sierra Nevada in the west and the Utah Uinta Mountains in the east, minimum temperatures have increased an average of 1 °C between 1910 and 2013 (Millar et al., 2015), and regional temperatures are expected to rise an additional 2–4 °C by the late 21st century (Scalzitti et al., 2016). This continental region is already known to be arid. The adjacent Sierra Nevada recently experienced the most extreme drought in recorded history, where high temperatures combined with low levels of precipitation to create strong, hot drought conditions, limiting soil moisture availability, and causing widespread forest mortality (Restaino et al., 2019; Young et al., 2017). Throughout the Great Basin, due to changes in precipitation phase (snow to rain), water runoff is expected to increase in the winter while decreasing in the spring and summer, ultimately leading to decreased water availability during the growing season and increased runoff during winter, outside of the typical growing season of sub-alpine tree species (Harpold et al., 2012; Melack et al., 1997).

Sub-alpine forests of the Great Basin are largely composed of Great Basin (GB) bristlecone pine (*Pinus longaeva* DK Bailey) and limber pine (*Pinus flexilis* James) (Fig. 1). While limber pine has a broad distribution across much of western North America over a wide range of elevations and forest types, GB bristlecone pine is limited to highly disjunct treeline stands in the mountains of the Great Basin. Due to the rain shadow of the Sierra Nevada, the Great Basin is a dry system of mountains with a Mediterranean to monsoonal weather pattern trend moving west to east. Wetter slopes in the eastern Great Basin are colonized by stands of Engelmann spruce (*Picea engelmannii* Parry), and quaking aspen (*Populus tremuloides* Michaux), while whitebark pine (*Pinus albicaulis* Engel) is found in parts of the northern and eastern Great Basin treeline. Great Basin bristlecone pine is famously known for its individual longevity, with some trees in the Great Basin approximating 5,000 years old, making those individuals the oldest nonclonal organisms living on earth (Brown, 2017; Schulman, 1958).

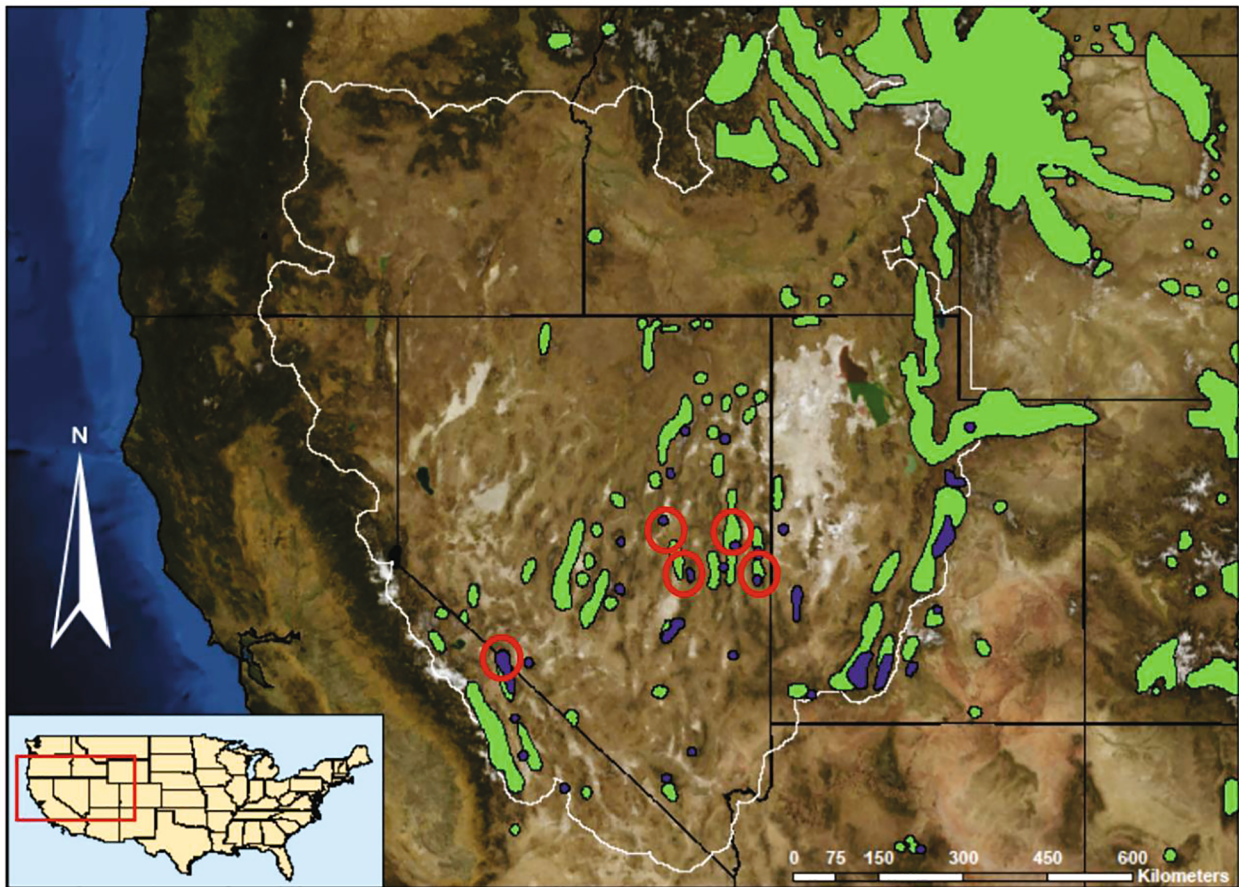


Fig. 1. The Great Basin region (outlined in white) is centered on the state of Nevada and is dominated at treeline by limber pine (green) and Great Basin bristlecone pine (purple). Nearly the entire extent of Great Basin bristlecone pine’s range falls within the Great Basin. Limber pine’s range extends northward into Canada. Red circles indicate the mountain ranges from where the seeds for this experiment came. From west to east: Boundary Peak, Mount Hamilton, Fish Creek Range, Cave Mountain, and Wheeler Peak. Species distribution vectors were downloaded from the USGS Little’s Range and FIA Importance Value Distribution Maps (Prasad and Iverson, 2003). These are meant as a general description and do not always reflect actual species distribution. The background map was downloaded from the USGS National Map Program (<https://www.nationalmap.gov/>) and accessed using ArcGIS. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Experimental design

We collected mature seed cones from mixed limber pine and GB bristlecone pine treeline stands from five Great Basin mountain ranges (Fig. 1). From each stand, we collected seed cones from 11 individuals per species per stand. The cones were dried and opened naturally under greenhouse conditions. We performed seed viability tests through a custom viability tester that blows the seeds varying distances with full, viable seeds being blown the least distance. We cold-stratified 100 seeds per individual for a total of 5,500 viable seeds per species (11,000 total seeds) by placing them in aerated water for 36 h and then air drying them at ambient room temperature for seven hours. We then stored the seeds at 2 °C for 17 weeks. We sowed the seeds into pre-watered Sunshine #4 Aggregate Plus™ soil in 164 ml (10in³) SC10 supercells which were placed into 98-cell racks. To approximate the germination season, we sowed the cold-stratified seeds for all experiments on June 29th, 2015. For all waterings, we watered the seedlings to complete soil saturation of the tube. To examine drought stress at three different early life stages, we then placed the seeds randomly into three experiments: post-germination, the first year of establishment (first-year), and the second year of establishment (second-year).

For the post-germination experiment, we placed 1537 seeds/species into three treatments: control, low water, and no water immediately after sowing in the pre-watered soil (Table 1). We placed the cells into 98-cell racks, which we regularly rotated within the treatment area. All

Table 1
Number of each seed (post-germination) or seedling (first- and second-year) subjected to each treatment in each experiment. Numbers in parentheses are the number of seedlings that were measured for height and diameter for each treatment and species.

Experiment	Treatment	Bristlecone pine (n)	Limber pine (n)
Post-germination	control	329	329
	low water	604	604
	no water	604	604
First-year	control	329 (208)	329 (171)
	3rd watering	531 (179)	498 (204)
	5th watering	519 (177)	499 (203)
	no water	520 (204)	501 (184)
Second-year	control	134 (134)	183 (179)
	3rd watering	437 (193)	424 (183)
	5th watering	430 (217)	428 (167)
	no water	480 (9)	385 (5)

seeds in all treatments were mist watered daily until most of the seeds emerged and the seed coat was shed which we determined to be 14 days. Following emergence, we watered the control seedlings weekly. The low water seedlings were watered every second control watering, or every two weeks. The no water treatment seedlings were never watered after the 14-day emergence period.

For the first-year experiment, we treated all seeds as controls during

the emergence period (mist watered daily for 14 days) and then we watered them weekly. After 46 days, we called the living seedlings “established” based on growth of true leaves and removed the non-emerged or dead first-year experiment seedlings. We placed the remaining 3726 living seedlings into one of four treatments: control, third watering, fifth watering, and no water (Table 1). We placed the seedling cells into 98-cell racks, which we regularly rotated within the treatment area. The control seedlings were watered weekly with the third and fifth watering treatments watered every third or fifth week, respectively. The no water seedlings were not watered after the treatments began.

For the second-year experiment, we treated all seeds and subsequent seedlings as controls until December, at which point we moved them outside to cold-harden the seedlings. In March, we moved 2901 living seedlings back into the greenhouse and placed them into the same treatments as the first-year seedlings: control, third watering, fifth watering, and no water (Table 1). We placed the seedling cells into 98-cell racks, which were regularly rotated within the treatment area.

We monitored seedlings for survival once per week and recorded a seedling as dead on that date if no green remained on any part of the leaves. For the first-year seedlings, we measured the stem diameter and seedling height for a random subset of the seedlings under each treatment at the start of the treatment and remeasured after 24 weeks. For the second-year seedlings, we measured starting height and diameter two weeks after the start of treatment and remeasured 30 weeks after treatment. Because of this delayed initial measurement, many of the second-year/no water seedlings had died before they could be initially measured. None of the no water seedlings survived to remeasurement and so are excluded from the analysis (Table 1). We did not measure stem height or diameter in the post-germination experiment. These experiments were conducted at the USFS Institute of Forest Genetics in Placerville, CA which provided greenhouse water and temperature controls for our experiments.

2.3. Statistical analysis

We fit generalized linear models (GLMs) for each establishment period using drought treatment and seedling species as predictor variables to examine their effects on the response variables of height growth, diameter growth, and survival duration. Height growth, diameter growth, and survival duration were all log transformed to better fit the assumptions of normality, and assumptions for parametric modeling were verified using diagnostic plots. We used limber pine under the control watering scheme as the baseline group for all statistical modeling. To examine treatment and species effects, we used ANOVA models fitting both additive and interactive models, and used Tukey's HSD for pairwise comparisons between species with treatments. We determined the best fit model using the Akaike Information Criterion ($\delta AIC < 2$). Since survival durations were only recorded at the point of death, all individuals lacking a recorded mortality date were deemed to have survived that life stage period and were assigned a maximum survival duration to the final day of that experimental period. Measured from the onset of treatment, those survival duration values were 115 (post-germination), 462 (first-year), and 239 (second-year) days.

To model survival, we converted survival durations to a binomial survival scheme and fit binomial GLMs for each establishment period to examine the effects of drought treatment and species on overall term survival. Fitting GLMs on survival duration data broadly across all establishment periods was deemed inappropriate since survival durations were assigned for individuals that survived each period. However, in the first-year experiment, nearly all survival duration data for the no water drought treatment and both species' interquartile range (including at least 75% of the data) for the fifth watering scheme fell below the first-year experiment's duration. Here, we used a GLM on survival duration data for the no water and fifth watering schemes of the first year. All visualizations were created using the library *ggplot2*

(Wickham, 2009) with colorblind-friendly *viridis* palettes (Garnier et al., 2018).

3. Results

3.1. Growth

In the first year of establishment, we found an interaction between treatment and species ($p = 0.002$) with the interaction model outperforming all other models ($\delta AIC = 8.099$). Increasing drought severity had an increasingly negative effect on height growth for the third and fifth watering treatment (both $p < 0.001$). Overall, limber pine had somewhat lower height growth than GB bristlecone pine (Fig. 2a, $p < 0.031$). We found no difference between limber and GB bristlecone pine height growth in the third or fifth watering treatments, however in the control treatment, limber pine showed lower height growth than GB bristlecone pine ($p = 0.009$). Under the fifth-watering condition, limber pine had a positive interaction, where limber pine's growth was higher than expected when considering the other combinations of pine species and drought treatment ($p < 0.001$). We also found an effect of treatment on diameter growth ($p = 0.003$), however species did not have an effect ($p = 0.209$). Only the third watering treatment was different from the control ($p < 0.001$).

In the second year of establishment, we found an effect of treatment ($p < 0.001$) and species ($p < 0.001$) on height growth, with no significant interactions ($p = 0.189$). The fifth watering treatment had a negative effect on overall height growth ($p = 0.002$), and limber pine had higher height growth (Fig. 2a, $p < 0.001$), with limber pine showing greater height growth under every treatment (Fig. 2b). For diameter growth, we found an effect of treatment ($p < 0.001$) and species ($p < 0.001$), with no significant interactions. Both the third and fifth watering treatments had negative effects on diameter growth (3rd: $p < 0.002$, 5th: $p = 0.062$). Limber pine showed greater diameter growth under every treatment ($p < 0.001$).

3.2. Survival

During the post-germination period, we found an effect of treatment ($p < 0.001$), but not species ($p = 0.351$), on seedling survival. However, we did find an interaction between treatment and species ($p = 0.014$), with the interaction model outperforming the additive model ($\delta AIC = 4.595$). We found a positive interaction under the low water treatment, where the observed seedling survival in limber pine was higher than expected based on the other species and drought treatment combinations ($p = 0.011$). Unsurprisingly, the no water treatment had a strongly negative effect on seedling survival ($p < 0.001$). Overall, limber pine had slightly, and insignificantly, lower survival than GB bristlecone pine ($p = 0.100$) with no differences in survival between the species under the control, low water, or no water treatments. The last individuals to survive the no water treatment were two GB bristlecone pine seedlings after more than one month of never receiving any water.

In the first year of establishment, we found an effect of treatment ($p < 0.001$) and species ($p < 0.001$) on survival, as well as an interaction between treatment and species ($p = 0.001$). The interaction model outperformed the additive model ($\delta AIC = 9.625$). We found a negative relationship between drought severity and survival (3rd: $p = 0.048$, 5th: $p < 0.001$, no water: $p < 0.001$). While we found no end-term survival difference between species when considering all treatments, limber pine generally appeared to have earlier onset mortality than GB bristlecone pine (Fig. 3a). Using pairwise analysis, we found no difference in limber pine and GB bristlecone pine survival under the no water treatment, which is due to all individuals of both species ultimately dying before the end of the first-year term yielding effective survival rates of zero. Despite this, it is still important to note that limber pine experienced an earlier drop in survival (Fig. 3a). GB bristlecone pine had higher survival under the third watering ($p = 0.003$) and fifth watering ($p < 0.001$),

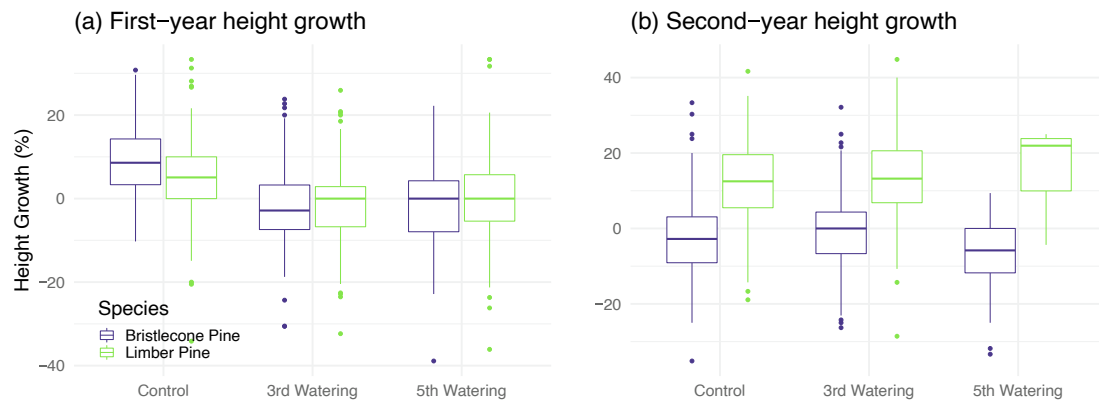


Fig. 2. Height growth rates for Great Basin bristlecone pine (purple) and limber pine (green) across drought treatments during the first (a) and second (b) year of establishment. Each point is the percent change in height measured between the beginning and the end of the treatment period. The 'no water' treatment is omitted as no measured seedlings survived to the end of the treatment period. Boxes represent the interquartile range (25% to 75% of data points), with the solid line indicating the median value. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

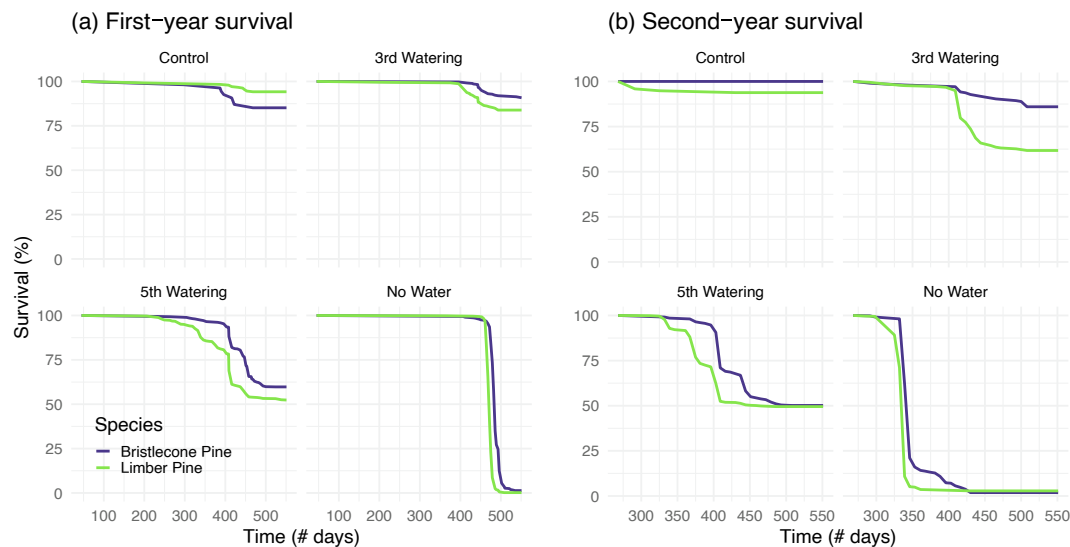


Fig. 3. Survival plots for Great Basin bristlecone pine (green) and limber pine (purple) across varying drought treatments during the first and second year of establishment. The days represent the number of days since sowing. Lines track the percent of the original seedlings alive through the progression of days during each term. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

while limber pine had higher survival under the control ($p = 0.007$), with GB bristlecone pine experiencing a drop in survival earlier than limber pine. In the fifth watering treatment, we found an observed negative interaction in which limber pine had lower first-year survival than expected when considering the other combinations of species and drought treatments ($p = 0.008$).

In the second year of establishment, we found an interaction between treatments and species on end-term survival ($p = 0.001$) with the interaction model outperforming the additive model ($\delta\text{AIC} = 10.247$). There was an increasingly negative effect on survival with increased drought severity (Fig. 3b, 3rd $p = 0.051$, 5th $p < 0.001$, no water $p < 0.001$). GB bristlecone pine had higher end-term survival under the control ($p = 0.010$) third watering ($p < 0.001$) and fifth watering treatments ($p < 0.001$). There was no observed difference in end term survival between species within the no water treatment as all individuals died, however limber pine generally showed mortality earlier than GB bristlecone, a trend that occurred in all treatments (Fig. 3b).

3.3. Survival duration

In the post-germination and second-year experiments, the survival

duration of seedlings decreased with increasing time between watering for both species (Fig. 4a,c). However, in the first-year experiment, both limber pine and GB bristlecone pine seedlings under the no water treatment had longer average survival durations than seedlings in the fifth watering treatment ($p < 0.001$, Fig. 4b). Despite having shorter average survival duration (Fig. 4b), seedlings of both species in the fifth watering treatment had higher overall long-term survival than seedlings in the no water treatment ($p < 0.001$). In the first year, while the no water seedlings had no end-term survival, the average survival duration was surprisingly and consistently high for both species.

4. Discussion

Our results point to three key findings. The first is that we can accept our first hypothesis that an increase in drought stress led to a higher mortality rate as well as lower growth rates in both species. The second key finding is that seedlings in later life stages were more susceptible to drought stress, especially extreme drought stress. This finding causes us to reject our second hypothesis that later life-stage individuals would have higher survival rates than earlier life-staged individuals in response to drought. The third key finding is that while limber pine had higher

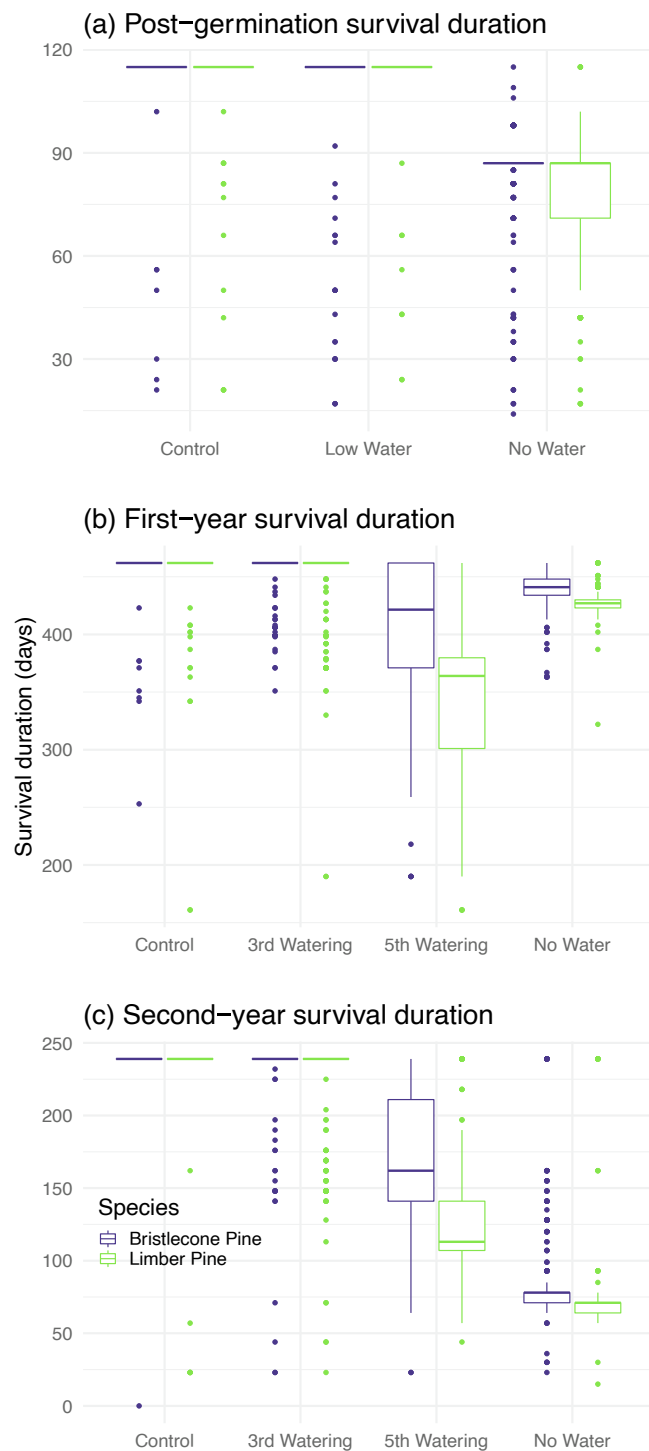


Fig. 4. Survival durations for Great Basin bristlecone pine (purple) and limber pine (green) across varying drought treatments during the post germination period and the first and second year of establishment. Each point is a single count of mortality. Boxes represent the interquartile range (25% to 75% of data points), with the solid line indicating the median value. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

height and diameter growth than GB bristlecone pine under drought conditions, it also had higher mortality, causing us to reject our third hypothesis that limber pine would have higher survival than GB bristlecone pine in drought conditions.

While these findings point to interesting differences between species

and early life stages in response to drought, some caution is required in interpreting these results. The first is inimical to any artificial experiment in that a greenhouse study like this narrowly approximates natural conditions. In an effort to standardize growing conditions to specifically target the effects of differential water availability on seedlings, most conditions are not found in natural settings. For example, we used a standard potting soil, but these trees both naturally grow on very specific soil types that have strong effects on which species dominates (Smithers et al., 2018; Wright and Mooney, 1965). The differences in soil type preferences may be a function of that soil type's ability to hold water (Smithers, 2017), but there are likely other differences in how soil characteristics interact with seedling success. Seedlings growing near the treeline ecotone are strongly limited by microclimate extremes. In summer, soil surface temperatures can be very high while winter conditions can be brutally cold (Smithers, 2017). In order to survive, seedlings must survive this gauntlet, but this experiment did not include these kinds of extremes. All pines growing in natural conditions are also ectomycorrhizal obligates with ectomycorrhizal colonization varying considerably among soil types and among species (Shemesh et al., 2020). Conifer seedlings with ectomycorrhizal associates are far more able to fix carbon under drought conditions (Parke et al., 1983). Pine seedlings also extend their roots deeply into the soil and into small rock fissures where water can collect. These seedlings were confined to the container in which they were sown and by the second-year experiment, the roots had filled the entirety of the cone volume. This likely caused faster dry-down of the soil after watering, making the seedlings in later life stages appear to be more susceptible to drought than they might be naturally. In some species-treatment combinations we found negative median growth rates. While soil settling, measurement errors, or other artifacts of the greenhouse experiment may explain this, stems can also considerably “shrink” under drought conditions (Brække and Kozłowski, 1975; Ogigirigi et al., 1970). Still, the large numbers of individuals, especially those of bristlecone pine, that had negative growth over the treatment period remains an unexplained curiosity from this study.

4.1. Growth

We found that the effects of drought on growth depended on the age of the seedlings as well as the species. In the first year of growth, GB bristlecone pine showed slightly higher growth overall and under control conditions, but not for all treatments (Fig. 2a). In the second year, we found that drought led to large overall decreases in height growth. However, that decrease appears to principally be a function of the drought effects on limber pine (Fig. 2b). GB bristlecone pine showed consistent and relatively low height growth regardless of treatment, suggesting that growth in GB bristlecone pine is not as sensitive to water conditions as it is in limber pine. Even with plentiful water, GB bristlecone pine growth is relatively slow.

Limber pine's faster growth, at least in the second year, may give it an establishment advantage over GB bristlecone pine. Throughout the Great Basin, limber pine is advancing into novel territory at greater rates than GB bristlecone pine (Millar et al., 2015; Smithers et al., 2018). While limber pine may have other possible establishment advantages, such as its dispersal vector, Clark's nutcracker (*Nucifraga columbiana* Wilson) (Lanner and Vander Wall, 1980; Tomback and Kramer, 1980), limber pine's ability to grow relatively faster than GB bristlecone pine may be part of this advantage. On the contrary, GB bristlecone pine appears to be slower-growing, and equally slow-growing at varying levels of drought. This suggests the GB bristlecone pine's growth is less plastic than limber pine's making it both less able to take advantage of benevolent growing conditions, but possibly also less susceptible to longer drought effects (Barber, 2013; Beasley and Klemmedson, 1973; Connor and Lanner, 1990). This faster growth in limber pine appears to be even more pronounced in the second year of establishment. Limber pine also appears to have greater “memory” of water conditions in its physiological response (Liu and Biondi, 2020). Limber pine seedlings

show greater change in sap flow in response to the previous winter water conditions relative to GB bristlecone pine. Our study also adds evidence to limber pine having relatively greater plasticity in response to variable water availability while also showing the potential cost of that plasticity relative to GB bristlecone pine.

4.2. Survival

As expected, we found that survival decreased with drought stress in seedlings regardless of the seedling age. For both species, survival was generally lower for second-year seedlings than for first-year seedlings, and that under the more severe drought treatments, seedlings started dying earlier in the second-year experiment than in the first-year. Survival rates decreased overall with increasing drought stress. Limber pine also generally began mass mortality earlier than GB bristlecone pine and tended to have lower overall survival.

Under control conditions, first-year limber pine seedlings had higher survival rates than GB bristlecone seedlings, but under all other scenarios, there was either no difference between the species or GB bristlecone pine had higher survival. Coupled with the results from our growth studies, there appears to be a trade-off between growth and survival for these two species. Relative to GB bristlecone pine, limber pine appears to have higher growth while being more susceptible to mortality in the event of drought. This is especially apparent in the second year of growth when the seedlings had a higher capacity for growth but were more susceptible to mortality in longer periods of drought. Conifer seedling susceptibility to drought has been well established in a variety of forests throughout the western US (Andrus et al., 2018; Foster et al., 2020; Moyes et al., 2015) while soil moisture deficit has increased over the last century (Kroiss and HilleRisLambers, 2014; League and Veblen, 2006). Continued increases in soil moisture deficit in western US coniferous forests are highly likely. Given that both these species are famous for slow growth in dry growing conditions, it is interesting that the two species appear to take drastically different strategies that are likely to work in favor of one species over the other, depending on conditions. That being said, limber pine and GB bristlecone pine are both known for their drought tolerance relative to other conifers, even those found in Great Basin sub-alpine forests. Engelmann spruce, quaking aspen, and whitebark pine would likely have fared far worse than either of our focal species in these treatments and are likely even more at risk from increased drought stress.

These results have implications for predicting the future of sub-alpine forests in the Great Basin. Treeline advance can look different in different systems and species can have considerably different responses to change (Davis et al., 2020). Throughout the Great Basin, limber pine has an establishment advantage over GB bristlecone pine at upper treeline and other range boundaries (Millar et al., 2015; Smithers et al., 2018). At specific, possibly drier or lower sites, GB bristlecone pine may have an establishment advantage (Kilpatrick and Biondi, 2020). With limber pine forests often found in lower, drier forests than GB bristlecone pine forests, this is contrary to what might be expected. How these two species will establish relative to each other will likely depend strongly on the nature of precipitation trends as the climate continues to warm. For example, a warmer, drier climate in these forests may favor GB bristlecone pine establishment, while a warmer, wetter climate may favor limber pine establishment. This is not what we might expect by looking at adult tree distributions alone.

4.3. Severe drought stress tolerance

As expected, both species ultimately had zero individuals survive the no water treatment in both the first- and second-year experiments. Those seedlings were sown in wet soil (as were all treatments) but were never watered. Interestingly, in the first-year experiment, survival durations for both limber pine and GB bristlecone pine were higher in the no water treatment than they were in the fifth water treatment. The seedlings that

got a very small amount of water (fifth watering treatment) had shorter life spans than those that were never watered. While this observation was obvious in the first-year treatment, we did not observe it in the second-year or the post-germination experiments.

This finding suggests that there is some ability of the seedlings to severely curtail growth at that early life stage. It is possible that when a seedling receives no water, it has an ability to enter a kind of dormancy, slowing growth to a standstill. In this experiment we did not re-water our seedlings once mortality was recorded, so it is unclear if these “dormant” seedlings would be able to resume growth. Of note is the consistency observed within the no water seedlings. Not only did all these seedlings ultimately experience mortality, but the synchronicity of their survival durations relative to the other treatments were high. We observed this precision in both limber pine and GB bristlecone pine (Fig. 4), suggesting that this is a physiological mechanism in at least these two pine species. We do not know the actual cause of mortality, whether it was carbon starvation or hydraulic failure. Regardless of the proximal cause of death, the negative growth seen in other drought treatments suggest that carbon loss occurred in the drought-stressed seedlings.

In the fifth watering seedlings, the infrequent water was possibly enough to keep plant systems active and prevent the dormancy period, but not enough to sustain the seedlings through the full first-year period with the growth hastening mortality. The variability in survival durations was also much greater within the fifth watering seedlings, with many but not all experiencing mortality by the end of the term. Growth measurements relative to growth in the fifth watering treatment may have further supported our hypothesis of a dormancy period, but since all the no water treatment seedlings died before the end of term, we were unable to collect growth measurements for comparison.

In other conifer species, seedlings appear to be predetermined to prioritize short-term growth over long-term drought tolerance although there are differences among species in relative prioritization (Augustine and Reinhardt, 2019). Differences between pine and juniper species in how they balance growth versus drought are well known (Breshears et al., 2009; West et al., 2008) with physiological differences in tracheid structure and stomatal sensitivity determining the drought levels at which a seedling will limit water transport and growth. Given that limber pine and GB bristlecone pine live in roughly the same dry conditions, it would be reasonable that the two species share a threshold for drought dormancy. However, to date there is scant evidence that conifer seedlings prioritize drought survival over growth, even in drought-exposed species (Augustine and Reinhardt, 2019). Limber pine and GB bristlecone pine, growing in very dry mountains, may be an exception to this rule.

4.4. Conclusions

In response to drought, limber pine seedlings generally had higher growth than GB bristlecone pine, but it came at the cost of higher mortality. Limber pine seedlings generally died earlier than GB bristlecone pine and at a higher overall rate. Somewhat strangely, in the first year of establishment when seedlings received no water at all, both species showed a later mortality response and greater survival durations than a treatment with more water. This indicates that there is some ability for both limber pine and GB bristlecone pine to “shut down” in response to extreme drought to avoid drought-induced death.

The difference in species response to drought stress during the establishment phase indicates different life history strategies between these two species growing in the cold, dry Great Basin mountains. Depending on the soil water availability associated with warming temperatures in the Great Basin, which remains mostly unclear, our results suggest different demographic trajectories of species dominance between limber pine and GB bristlecone pine as seedlings establish above historical treeline. While a warmer, wetter future may favor limber pine, a warmer, drier future may favor GB bristlecone pine.

CRediT authorship contribution statement

Brian V. Smithers: Conceptualization, Methodology, Software, Formal analysis, Investigation, Resources, Visualization, Supervision, Project administration, Funding acquisition. **Franklin Alongi:** Methodology, Software, Formal analysis, Data curation, Visualization. **Malcolm P. North:** Conceptualization, Methodology, Resources, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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