

RESEARCH ARTICLE

The Importance of Tree Regeneration for Maintaining Mountain Forest Ecosystem Services Under Global Change

Overstorey mortality promotes juvenile piñon pine growth during favourable weather at cooler, wetter sites

Edward M. Hill¹  | Troy W. Ocheltree¹ | John B. Bradford²  | Alexandra K. Urza³  | Miranda D. Redmond⁴

¹Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, Colorado, USA

²Southwest Biological Science Center, U.S. Geological Survey, Flagstaff, Arizona, USA

³USDA Forest Service, Rocky Mountain Research Station, Reno, Nevada, USA

⁴Department of Environmental Science, Policy, and Management, University of California Berkeley, Berkeley, California, USA

Correspondence

Edward M. Hill

Email: edwardmhill@gmail.com

Funding information

Colorado Mountain Club Foundation; BYU Charles Redd Center for Western Studies; Rocky Mountain Research Station; National Institute of Food and Agriculture, Grant/Award Number: 1018490

Handling Editor: Tom Wohlgemuth

Abstract

1. Hotter droughts have resulted in widespread tree die-off events globally, frequently leading to regeneration failure. Dry forest recovery often depends on the growth and survival of extant juvenile trees. However, it is unclear how microenvironmental changes following overstorey tree die-off affect juvenile trees, particularly in dryland systems where tree recruitment is typically limited by water availability and heat stress.
2. We simulated an overstorey tree die-off event by girdling trees in piñon-juniper woodlands across the south-western United States. We sampled juvenile piñon pine growth from live and dead overstorey treatments across six study sites spanning a regional latitudinal gradient and local elevational gradients. We examined how juvenile branch and needle growth differed between live and dead overstorey treatments, and whether responses varied with weather conditions and juvenile tree size following overstorey mortality.
3. We found greater juvenile branch and needle growth under dead compared with live overstorey trees for 2 years following overstorey mortality at mid- and high-elevation sites which are typically cooler and wetter than the other sites. These observed growth releases were contingent on favourable post-mortality weather conditions. Higher growth under dead overstorey occurred at sites experiencing near-average climatic water deficits compared with sites experiencing above-average climatic water deficits. Growth at all sites increased from the first to second year after overstorey mortality. Across sites, growth was unrelated to juvenile tree size.
4. *Synthesis.* Our results underscore differentiation in juvenile responses to overstorey tree die-off driven by local site conditions and weather across the range of *Pinus edulis*. Overstorey mortality resulted in consistently higher juvenile growth only at climatically favourable sites and during favourable weather, while unmeasured microsite differences could help account for variation observed at the hottest and driest site. Results from less climatically favourable sites suggest that overstorey trees neither directly limit nor facilitate juvenile growth,

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2026 The Author(s). *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

though further study over longer timeframes is needed to resolve the pace and magnitude of potential recovery or decline. Overall, juvenile vigour may be promoted following overstorey mortality only in a narrow spatial (site) and temporal (weather) environmental context, suggesting additional vulnerabilities for piñon populations under more arid conditions.

KEYWORDS

climate gradients, growth release, juvenile tree, piñon-juniper woodlands, tree mortality

1 | INTRODUCTION

Adaptations of tree populations to local climate variability and chronic stressors may shape their capacity to resist and recover from disturbances, such as heatwaves and droughts (Brodribb et al., 2020; Gazol et al., 2023). Changing climate conditions in many regions, especially dryland ecosystems, include more frequent occurrences of severe disturbances and exacerbate abiotic stresses in post-disturbance environments (Costanza et al., 2023). With rising temperatures and increasing atmospheric and soil drought in dryland systems (Bradford et al., 2020), forest and woodland communities may struggle to recover from increasingly common disturbances, such as extensive, drought-driven tree die-off events (Shriver et al., 2021; Xu et al., 2024). While understanding patterns and mechanisms of drought-related tree die-off globally is improving rapidly (Hammond et al., 2022; Xu et al., 2024), major knowledge gaps remain for understanding the near-term outcomes for extant juvenile trees, which are less susceptible to direct mortality and can persist after overstorey tree die-off (Camarero, 2021; Ma et al., 2023; Redmond et al., 2015).

For species that occupy broad ranges of environmental conditions, population adaptations to local environmental conditions often reflect broad climate gradients from warmer and drier to cooler and wetter locales (Dixit et al., 2022; Gazol et al., 2023). Local populations that typically experience more chronic stresses, such as heat and seasonal drought, may be better adapted to withstand post-disturbance environmental stress characterized by high incident light, temperatures and evaporative demand, which occur with overstorey removal or in situ mortality (Camarero et al., 2024; Guérin et al., 2020). Similarly, populations which typically experience lower mean temperatures or more consistent seasonal moisture availability may be more susceptible to suddenly elevated heat- or water-related stresses in post-disturbance environments (Candido-Ribeiro & Aitken, 2024; Redmond et al., 2017). Alternatively, a lack of morphological (e.g. greater root density) or physiological trait plasticity (e.g. water-use efficiency) may limit the capacity for trees from some populations to adjust to post-disturbance resource environments (Dixit et al., 2022; McBranch et al., 2019). The extent to which local tree populations may respond differently to post-disturbance conditions may also be mediated by co-varying site conditions, such as abundance of competing vegetation, and the intersection of interannual weather variation with population-level trait variation (Gazol et al., 2023; Vasey et al., 2023).

Juvenile tree sensitivity to climate change stressors is often interpreted from broad-scale, correlative demographic patterns inclusive of wide ranges of tree sizes (e.g. Dobrowski et al., 2015), or from controlled experiments with imposed heat and drought stress on specific life-stages (e.g. Rother et al., 2015). Relatively little is known about how juveniles respond in situ to stressors associated with post-disturbance environments, which reflect underlying complexities of resource-use plasticity and site characteristics, rather than expression of adaptations to specific stressors (Gazol et al., 2023; Grams & Andersen, 2007). Overstorey tree die-off can rapidly alter resource conditions for surviving juveniles, including greater extremes of temperatures and evaporative demand (De Frenne et al., 2021), but also higher light and potentially soil water and nutrient availability (Grossiord, Gessler, et al., 2018). Juveniles present in relatively more productive sites with higher tree densities may experience continued light competition due to shading from dead or surviving trees, whereas warmer and drier sites may experience higher degrees of abiotic limitation after the loss of facilitative tree cover (Phillips et al., 2024). Additionally, juvenile responses may vary based on size-related physical maturity (Boyden et al., 2009). While larger juveniles likely possess physical capacities to better access available resources than smaller juveniles, these larger individuals may also be more limited by greater metabolic maintenance costs (Camarero et al., 2024; Ma et al., 2023), or stronger temporal mismatch of carbon acquisition and investment (Cabon, 2026). In contrast, smaller juveniles may suffer from inadequate resource acquisition and resource-use efficiency (Augustine & Reinhardt, 2019; Forrester et al., 2022; Gyenge & Fernández, 2014).

In piñon (*Pinus edulis*)-juniper (*Juniperus* spp.) woodlands in the south-western United States, extensive drought-driven overstorey mortality has caused demographic pressures for piñon pine (Shriver et al., 2021), as new piñon regeneration relies on seed availability and facilitation by overstorey trees or nurse shrubs (Redmond et al., 2015, 2018; Redmond & Barger, 2013). Surviving juvenile trees following overstorey die-off events therefore represent a crucial reservoir for woodland regeneration and development, providing the basis for woodland resilience. Yet piñon-juniper woodlands span a wide range of environmental conditions, broadly differentiated by temperatures and the relative influence of summer monsoon (vs. winter-dominated) precipitation (Falco & Waring, 2020; Samuels-Crow et al., 2023), and locally through pulse-precipitation events and shallow soil water dynamics (Kannenberget al., 2024; Romme et al., 2009). Such wide

gradients may lead to variable outcomes for juveniles following tree die-off. Observational studies have established patterns of adult piñon growth sensitivities at different sites to climate variation (e.g. Redmond et al., 2017), and differences in competitive or facilitative spatial associations of juveniles with overstorey across local edaphoclimatic gradients (Redmond et al., 2015). Additionally, many prior studies of adult piñon trees in similar environments have demonstrated strong influences of water limitations and heat on shoot growth, needle emergence and other related growth and physiological responses (e.g. Adams et al., 2015; Grossiord et al., 2017; Guérin et al., 2018). Because juveniles face more open and exposed conditions following overstorey die-off events, interactions among weather patterns, general site conditions and local population adaptations result in substantial uncertainty about growth responses of surviving juveniles across the range of piñon-juniper woodlands (Vasey et al., 2022, 2023).

To assess the effect of overstorey tree mortality on extant juvenile trees across different populations of piñon pine, we conducted a tree mortality experiment by girdling overstorey trees to simulate a die-off event at six sites that span regional (latitudinal) and local (elevational) environmental gradients. We compared growth responses of juvenile trees spanning a range of sizes under live (i.e. control) and dead (i.e. girdled) overstorey plots at our study sites over 2 years. Our objectives were to (1) understand how growth of juvenile piñon trees is affected by overstorey tree mortality across populations that span broad climatic gradients, (2) evaluate year-to-year growth responses in relation to corresponding weather variation and (3) assess the influence of juvenile size, as a proxy for resource acquisition and stress tolerance, on juvenile growth responses to overstorey mortality. With regard to these objectives, we hypothesized that (1) growth of juveniles would be greater after overstorey mortality at cooler and wetter study locations, (2) positive growth responses after overstorey mortality would be pronounced in cooler and wetter years of study, while limited growth (compared with live overstorey plots) would occur in warmer and drier years of study, and (3) growth would increase with juvenile tree size. Understanding juvenile responses to overstorey mortality, and variation among populations, is important for anticipating changes in local dryland forest and woodland communities, and can facilitate targeted management towards sensitive or priority populations, or away from areas of expected population extirpation (Noel et al., 2023). Using a replicated tree mortality experiment across environmental gradients, we aim to advance understanding of the outcomes of overstorey disturbance on juvenile trees under varying conditions.

2 | MATERIALS AND METHODS

2.1 | Regional and local study locations

We selected three regional study locations across the geographic distribution of two-needle piñon pine (*Pinus edulis*) (Figure 1) based on differences in climate (Figure 2; tabular comparisons are shown in Table S1). At these locations, with permission from local management

agency offices (Bureau of Land Management and US Forest Service), we established study sites spanning local elevational gradients of climate and woodland tree density (Falco & Waring, 2020) where piñon pine was dominant. We originally established sites at 'low', 'mid' and 'high' elevations, but we dropped high-elevation study sites from two locations due to safety concerns and wildfire impacts, as well as one low-elevation site where piñon juvenile abundance was insufficient for sampling. Our resulting six study sites included: low- and mid-elevations at our southern location in Arizona ('AZlow' and 'AZmid'); low-, mid- and high-elevations at our mid-latitude study location in south-western Colorado ('SCOl low', 'SCOm id' and 'SCOhigh'); and, mid-elevation at our northern location in north-western Colorado ('NCOmid'). The latitudinal and elevational distribution of these sites generally follows a climatic gradient from warmer and drier conditions at more southern latitudes and lower-elevations, to cooler and wetter conditions at more northern-latitude and high-elevation sites, with monsoonal precipitation being greatest at more southern-latitude sites (Figures 1 and 2). However, the northernmost site (NCOmid) is typically drier than mid- and high-elevation sites at more southern latitudes (i.e. AZmid, and SCOm id and SCOhigh; Figure 2). During our study, sites generally experienced warmer and drier conditions in year 1 (2020), with especially hot and dry weather in AZ and NCO, while subsequent years 2 and 3 (2021 and 2022) were generally average or wetter-than-average compared with long-term conditions at these sites (Figure 2).

All of our sites were small (~2 ha in size) and similar in structure in an effort to reduce plot to plot variability. Within each site, plots were topographically similar (e.g. elevation varied <5 m and estimated slope varied <15 percent, on average) and within the same or similar (in the case of SCOhigh) soils types according to Soil Survey Geographic Database (SSURGO) soil classifications (see Table S1 for details).

2.2 | Experimental design and field sampling

We designed an experiment to compare the growth of piñon pine juveniles occurring beneath and adjacent to live and dead overstorey trees, first identifying healthy piñon pine-dominated stands, establishing control and mortality (girdled) treatments in randomly selected groups of trees, and measuring juvenile growth following our mortality treatment. In the summer of 2019, we established 30 plots under live overstorey woodland cover at each of our six study sites. Plots were centred around individual, dominant piñon trees ('focal tree') that appeared healthy ($\geq 90\%$ live green foliage, no indications of decline in health). Selected focal trees were at least 10 m apart and no plots were established on slopes greater than 15%. To quantify overstorey woodland structure at each plot (Table S1), we measured stem diameter at root collar (or, basal diameter; hereafter, 'DRC') of all adult trees (≥ 9.0 cm DRC) within 7 m of each focal tree stem, which was approximately 1.25 times the height of focal trees, on average. We also measured juvenile trees (0.3–8.9 cm DRC) in the same plot area as overstorey structure, recording DRC and

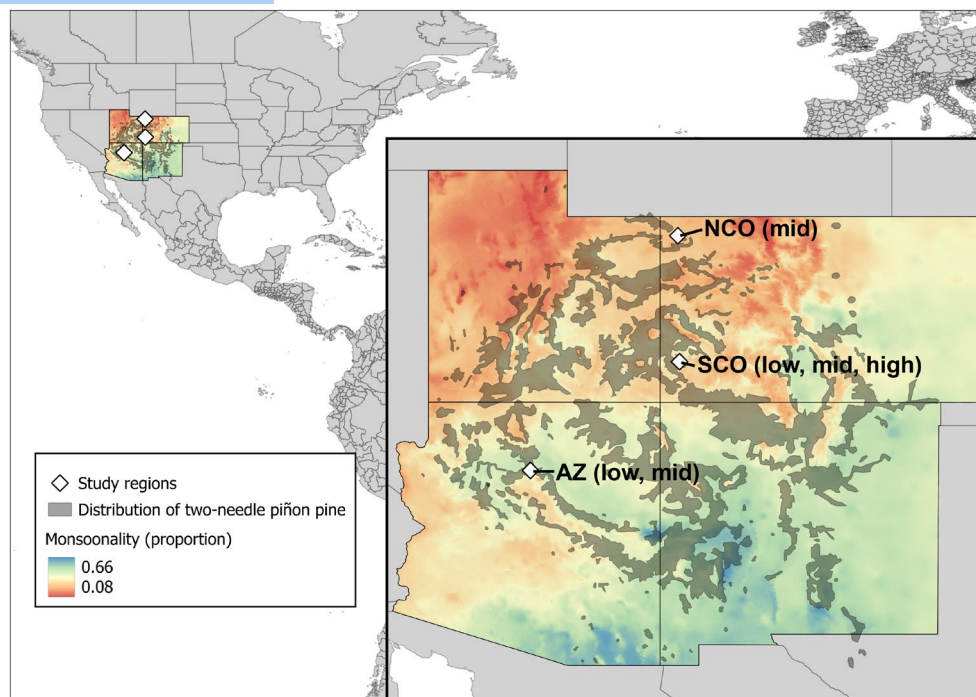


FIGURE 1 Study regions (white diamonds) relative to the distribution of two-needle piñon pine (*Pinus edulis*; grey shading, inset map; Cole et al., 2011). We established sites across a latitudinal gradient, within the geographic distribution of piñon pine, which reflected regional differences in climate, notably the prevalence of monsoon precipitation (colour gradient in inset map). Regions included Arizona (AZ), southern Colorado (SCO) and northern Colorado (NCO). Within the SCO and AZ region, study sites span an elevational gradient (not shown in map) to capture local environmental variation, including low- and mid-elevations in AZ (AZlow and AZmid), low-, mid- and high- elevations in SCO (SCOlow, SCOMid and SCOhigh), with only one site in NCO (NCOMid, occurring at a comparable mid-elevation).

location (distance and approximate azimuth in relation to each focal tree) to identify juveniles for subsequent sampling and to calculate juvenile competition indices (see below). After establishing plots, we randomly assigned each to a treatment of control (live overstorey) or tree mortality (dead overstorey). Our objective with the tree mortality treatment was to create environmental conditions similar to the understorey following drought-induced mortality of overstorey piñon trees. In the winter of 2019–2020 (~late November–early March), we girdled overstorey piñon trees (≥ 9.0 cm DRC) in each tree mortality treatment plot. The pace of mortality and the extent to which overstorey trees retained dead needles differed somewhat across sites and years in which growth was studied (2021 and 2022; Figure 3). We reviewed the effects of needle retention on growth in our models (described below), but because it was highly collinear with our overstorey treatment categories and did not change other results in our models, we report the results with needle retention excluded.

In this study, we focused our resources and sampling efforts on capturing potential piñon pine juvenile growth differences between live and dead overstorey treatments across a broad set of site conditions (Table S1). We used plot-level information from overstorey and juvenile tree structure sampling to approximate plot-plot variation in our analyses (described in analyses below; and see Table S1). We focus our study on piñon pine juvenile growth responses because this species is largely more vulnerable to drought-induced

mortality events and regeneration failures (Redmond et al., 2023; Shriver et al., 2021, 2022), it is the predominant species at our sites (Table S1), and because growth rates can be readily assessed using interannual bud scale scars, unlike juniper.

2.3 | Growth sampling

For growth measurements, we located piñon juveniles in our plots across all sites that spanned a wide range of size classes (from 0.3 to 8.9 cm DRC; mean $3.1 \text{ cm} \pm 2.5$, median 2.2 cm), which appeared healthy with no evident signs of stress or decline. In late September 2022, we sampled growth of individuals on lateral branches and needles, as we expected branch and needle growth to reflect relative resource availability (Guérin et al., 2018; Magnin et al., 2017; Sprugel, 2002) in contrasting live and dead overstorey treatment plots. For each individual juvenile tree, we randomly selected three branches to measure from the middle section of the crown area (Guérin et al., 2018; McBranch et al., 2019), though for smaller individuals we were sometimes limited to one or two branches for measurements. We measured annual growth using interannual bud scars, induced by the initiation of growing season phenology, as identifiers between years of growth (Adams et al., 2015). We took corresponding needle length measurements for each year of branch growth, using the average length of three needles per year (Adams

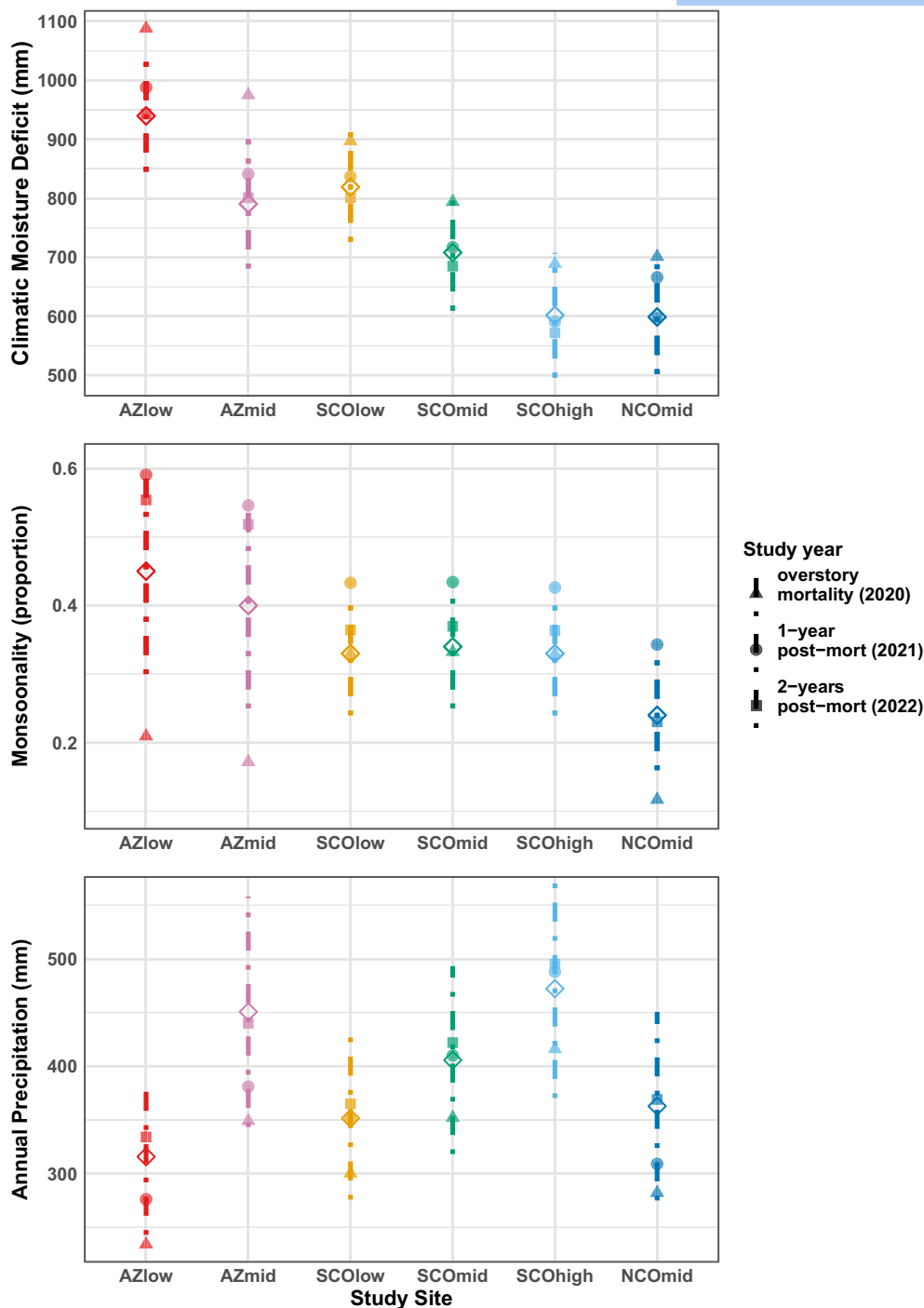


FIGURE 2 Comparisons of climate averages and weather conditions during study years 2020–2022 across study sites. Thirty-year climate averages are represented by open diamonds with corresponding lines representing 1 standard deviation above and below the mean. Weather conditions for each year of study are shown with solid points (overstorey mortality initiated in the winter of 2019–2020; 2021 and 2022 are 1- and 2-years post-mortality, respectively, when juvenile growth was measured). Climate variables include climatic moisture deficit (Hargreaves climatic moisture deficit, CMD, top panel), monsoonality (middle panel) and annual precipitation (bottom panel). Additional cross-site climate comparisons can be found in Table S1. All data were obtained from ClimateNA, <https://climatena.ca/>. Site codes: AZlow = low-elevation, northern Arizona; AZmid = middle-elevation, northern Arizona; SCOLow = low-elevation, south-western Colorado; SCOMid = middle-elevation, south-western Colorado; SCOhigh = high-elevation, south-western Colorado; NCOMid = middle-elevation, northern Colorado.

et al., 2015; Grossiord et al., 2017). To capture growth trends prior to our experiment, we attempted to measure growth back to the year (inclusive of) 2015, though we were sometimes limited to a

shorter time period with smaller trees. Mean growth record length was 7.1 years (± 1.4). For subsequent analyses, we averaged growth measurements for each year across all sampled branches for each

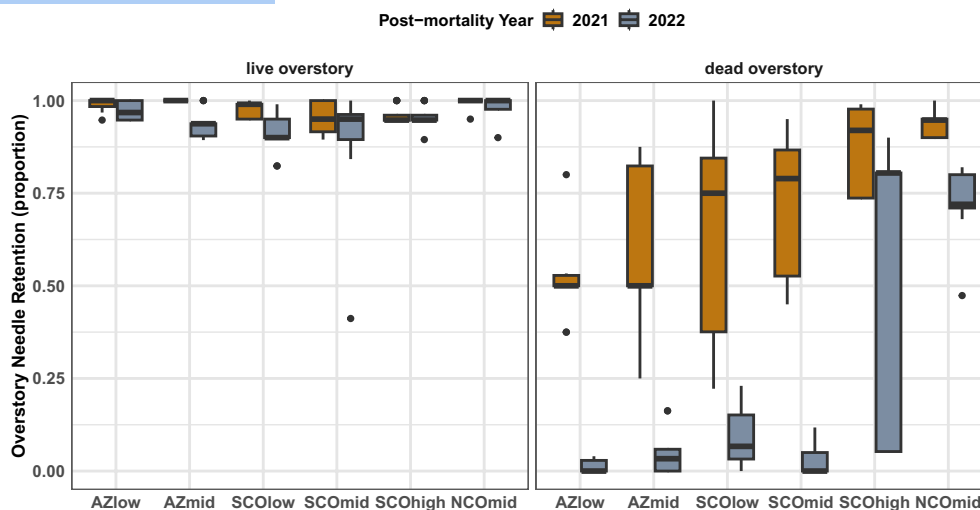


FIGURE 3 Proportion of overstorey needle retention among live (left) and dead (right) overstorey trees at each site. After inducing overstorey tree mortality in our experiment, loss of dead needles from these trees was variable across sites and years.

individual. Although we considered sampling height growth as a primary indicator of tree recruitment to upper canopy strata, we were unable to practically reach the taller juveniles in our study for accurate year-to-year height increments. We expected growth of lateral branches to sufficiently reflect distinctions in resource availability and subsequent growth patterns for juveniles in dead and live overstorey environments (Grams & Andersen, 2007; Gyenge & Fernández, 2014; Turrión & Bautista, 2025). Moreover, lateral branches and needles are frequently used as sampling units for estimating tree vigour in this species (e.g. Adams et al., 2015; Guérin et al., 2018; Kraklow et al., 2025).

2.4 | Analysis

To evaluate branch and needle growth of juvenile trees across a range of sizes following overstorey mortality, we calculated a growth ratio (branch growth ratio and needle growth ratio) that reflected the relationship of post-treatment growth relative to pre-treatment growth. For each full year of growth following overstorey mortality (2021 and 2022) we calculated:

$$GR_{iy} = \frac{\overline{\text{growth}}_{\text{post},ijk}}{\overline{\text{growth}}_{\text{pre},ilk}},$$

where GR_{iy} is the growth ratio (branch or needle) of an individual juvenile tree i in year y derived from the growth increment of the individual tree i in post – mortality year y ($y=1, 2$, including 2021 and 2022) averaged over k branches, relative to the average annual pre – treatment growth of the same individual and branches over l years sampled in the pre-treatment period. This follows similar approaches used in other studies (Cabon et al., 2023; Férriz et al., 2021) to assess growth responses after substantial changes in resource conditions (e.g. growth recovery following drought periods). We excluded 2020 growth

measurements from our calculations because we expected that the girdled trees were still actively dying during this time.

We used linear models ('stats' package in the R statistical computing environment; R Core Team, 2023), with maximum likelihood-based estimates of model coefficients, to assess influences on juvenile growth. We separately modelled 2021 and 2022 ('first-' and 'second-year' growth following overstorey mortality) branch and needle growth ratios. Consistent with our study objectives, we modelled branch and needle growth ratios as a function of the interaction between overstorey treatment (live and dead) and juvenile tree size (DRC) in all models. To avoid multicollinearity, in separate sets of models for each growth type (branch and needle) and year of growth (first- and second-year post-mortality), we included terms for the interaction of overstorey treatment and: (a) site, to examine patterns across populations (encompassing both differences in climate averages for each site and unmeasured site differences), and (b) post-treatment weather conditions, to understand how annual variability in weather affects juvenile growth responses in relation to overstorey mortality. We used annual climatic moisture deficit (CMD) (Hargreaves CMD, from climate data obtained from ClimateNA, <https://climatenana.ca/>, accessed on 3 January 2023; Wang et al., 2016), which captures ecologically relevant water deficit (Petrie & Savage, 2022). We calculated CMD differences ('dCMD') from the long-term (1991–2020) average to better assess the relative degree of abiotic stress in each year following treatment (Figure 2 and Table S1). Although both current and lag-year effects have been shown to affect growth in semi-arid forests in this region (e.g. Andrews et al., 2020; Guérin et al., 2018), we chose to keep models simpler by evaluating only one weather period for each branch and needle growth model. Branch growth in various pine species is especially influenced by weather conditions in the year of bud formation, which occurs in the year prior to branch elongation (Hover et al., 2017; Seidel et al., 2019); therefore, we evaluated the influences of prior-year weather for each year of growth for branch growth ratio models. In needle growth models, we evaluated the influences of same-year weather conditions as

measured growth, as needles form and grow in the year of branch elongation (Isik, 1990; Schiestl-Aalto & Mäkelä, 2017).

We included plot-level basal area and a juvenile competition index as fixed effects in our models to account for potential differences in growing conditions (e.g. light, moisture and temperature microclimates) and competitive environments represented by tree structural conditions. Juvenile competition was estimated by calculating the sum of squared size ratios between a focal juvenile (sampled for growth) and all neighbouring juveniles within a 1.5 m radius. This competition value is a variation on common size-ratio competition values (e.g. see index 6 in Looney et al., 2016), and specifically represents competition dominated by larger trees (assumed asymmetric competition). For model covariates whose distributions were highly skewed, including juvenile tree DRC, plot basal area and juvenile competition values, we log-transformed these variables to satisfy the assumptions of our linear modelling approach.

When we observed a significant interaction between site and overstorey treatment in models across sites, we used post hoc comparisons of marginal mean model predictions for multi-level

factors to evaluate differences across sites (within each overstorey treatment type) and within sites (between overstorey treatment type). We used the 'emmeans' function of the *emmeans* package (Lenth, 2023) with a false discovery rate *p*-value adjustment for multiple comparisons across sites, setting our significance threshold at $\alpha=0.05$. For all other effects in site and post-mortality weather models (see Table S2), we considered effects significant when confidence intervals did not overlap zero.

3 | RESULTS

3.1 | Branch growth ratios

3.1.1 | Site differences in branch growth responses to overstorey mortality (a)

Juvenile piñon pine branch growth ratios varied considerably across treatments (live and dead overstorey), sites and years (Figure 4). In

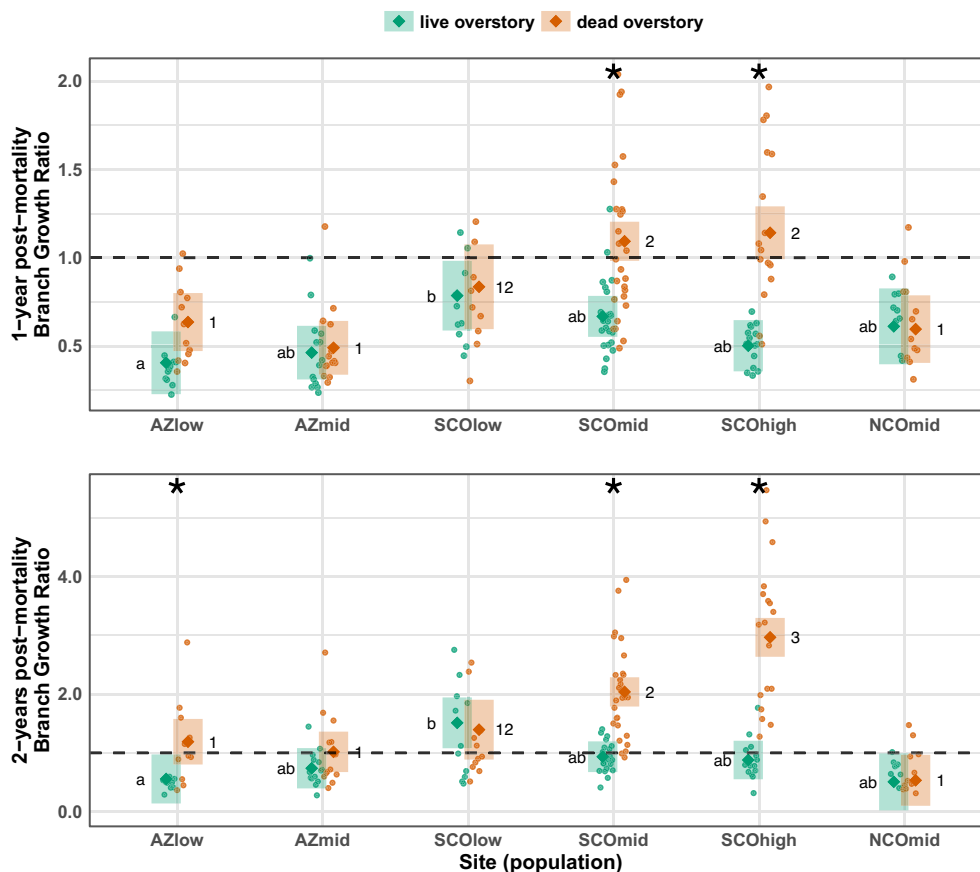


FIGURE 4 Branch growth ratios for the first (i.e. 2021; top panel) and second year (i.e. 2022; bottom panel) of growth following overstorey mortality across all sites, showing model results for the interaction of Site and overstorey treatment (live and dead). Points are tree-level observations, and modelled effects are shown with means (large diamond symbols) and 95% confidence intervals (shaded bars around large diamonds). Colours signify live (green) and dead (orange) overstorey treatments. Significance of pairwise comparisons of branch growth ratios between dead and live overstorey treatments within each site are denoted with an asterisk at the top of each plot. Post hoc comparisons of live overstorey treatments across sites and dead overstorey treatments across sites are denoted with letters and numbers, respectively, where shared values suggest no differences. The dashed horizontal line at 1.0 indicates a branch growth ratio value where post-mortality growth is equal to the mean of prior growth years.

both the first and second years (2021 and 2022) following overstorey mortality, branch growth ratios were greater in our tree mortality (dead overstorey) treatments compared with our control (live overstorey) at the mid- and high-elevation sites in south-west Colorado (SCOMid and SCOHIGH), our mid-latitude study area (Figure 4). Additionally, overstorey mortality resulted in increased growth ratios in the second year of growth at our low-elevation, southern-latitude Arizona site (AZLOW), but there were no effects of overstorey mortality on branch growth ratios in either year at the mid-elevation Arizona site (AZMID), the low-elevation south-west Colorado site (SCOLow) or our mid-elevation northern-latitude (NCOMid) site (Figure 4). Notably, in the first year following overstorey mortality, branch growth was higher than prior mean growth (i.e. growth ratio >1) in our tree mortality treatment at SCOMid and SCOHIGH and not at any other sites or in live overstorey (control) treatments. However, in the second year of growth after overstorey mortality, branch growth was higher than prior mean growth in our tree mortality treatments across all sites except NCOMid, whereas branch growth was below average (growth ratio <1) in live overstorey environments, except at SCOLow. In all branch growth models,

neither the interaction of juvenile tree size and overstorey treatment nor the main effect of juvenile tree size was significant (Table S2).

3.1.2 | Branch growth following overstorey mortality in relation to post-mortality weather (b)

In both years following overstorey mortality, we found a negative relationship between branch growth ratio and relative CMD in the year of bud formation (the year prior to the growth we measured), such that sites that were hotter and drier than normal (i.e. above-average CMD) had less branch growth (Figure 5). These relationships were much more pronounced in dead overstorey compared with live overstorey environments, which was predominantly driven by higher growth in dead overstorey environments at SCOHIGH and SCOMid where dCMD was lower compared with other sites in both years following overstorey mortality. Branch growth ratios generally did not have significant relationships with juvenile tree DRC and plot BA in post-mortality weather models, except for a smaller positive relationship of second-year branch growth ratios with increasing

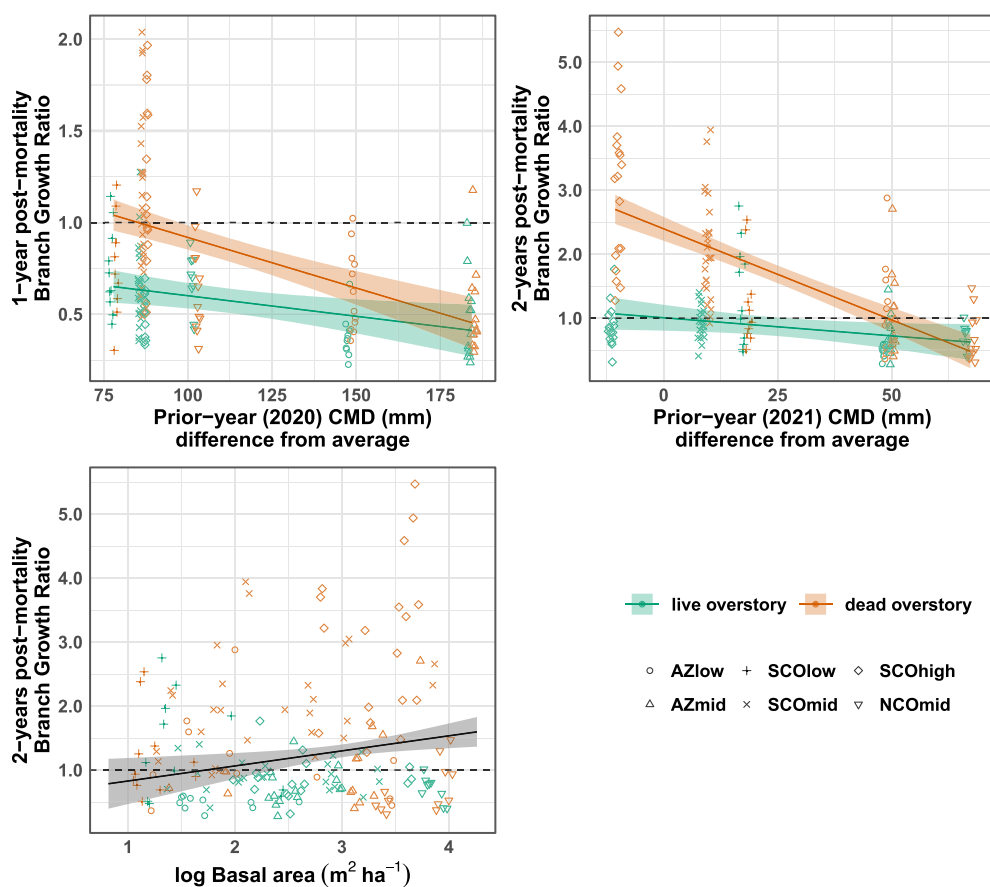


FIGURE 5 Relationship between branch growth ratio and post-mortality weather (top panels) and plot basal area (BA, bottom panel) across sites for first- (2021) and second-year (2022) growth following overstorey mortality treatments. We tested the effects of weather in years prior, when buds are formed, to a given year of measured growth. Colours signify live (green) and dead (orange) overstorey treatments. Shapes denote sites: AZlow = circle; AZmid = upward triangle; SCOLow = plus sign; SCOMid = x; SCOHIGH = diamond; NCOMid = downward triangle. The dashed horizontal line at 1.0 indicates a branch growth ratio value where post-mortality growth is equal to the mean of prior growth years.

plot BA (Figure 5, bottom panel). This relationship was weakened in part by lower growth at the NComid site despite generally higher plot BA than other sites.

3.2 | Needle growth ratios

3.2.1 | Site differences in needle growth responses to overstorey mortality (a)

Models of needle growth ratios reflected considerable variability across sites in the first year following overstorey mortality (2021) but showed more similarity across sites and overstorey treatments 2 years following overstorey mortality (2022) (Figure 6). As with branch growth ratios, needle growth ratios were higher in dead overstorey compared with live overstorey treatments at both mid- and high-elevation southern Colorado sites (SCOmids and SCOHights) in both years of measured growth following overstorey mortality. Needle growth ratios were also higher in dead overstorey treatments

compared with live in the first year following overstorey mortality for the low-elevation, southern-latitude site in Arizona (AZLow), while needle growth ratios were lower in dead overstorey treatments compared with live at the mid-elevation, northern-latitude site (NComid). Needle growth ratios in live overstorey treatments at AZLow were lower than all other sites except NComid, and needle growth ratios in live overstorey treatments were different at SCOmids compared with AZLow and NComid. Needle growth ratios in dead overstorey treatments at SCOmids and SCOHights were different than those at all other sites and different from each other, except for no difference between SCOmids and SCOLows. In the second year of growth, however, needle growth ratios in both live and dead overstorey treatments generally increased across AZLow, AZMids and NComid such that few cross-site differences occurred. Similar to branch growth, needle growth in the second year following overstorey mortality was mostly higher than mean growth in prior years (growth ratios >1), except in live overstorey treatments at AZLow and SCOHights, on average. No significant relationships occurred with juvenile tree DRC and plot BA in either year (Table S2).

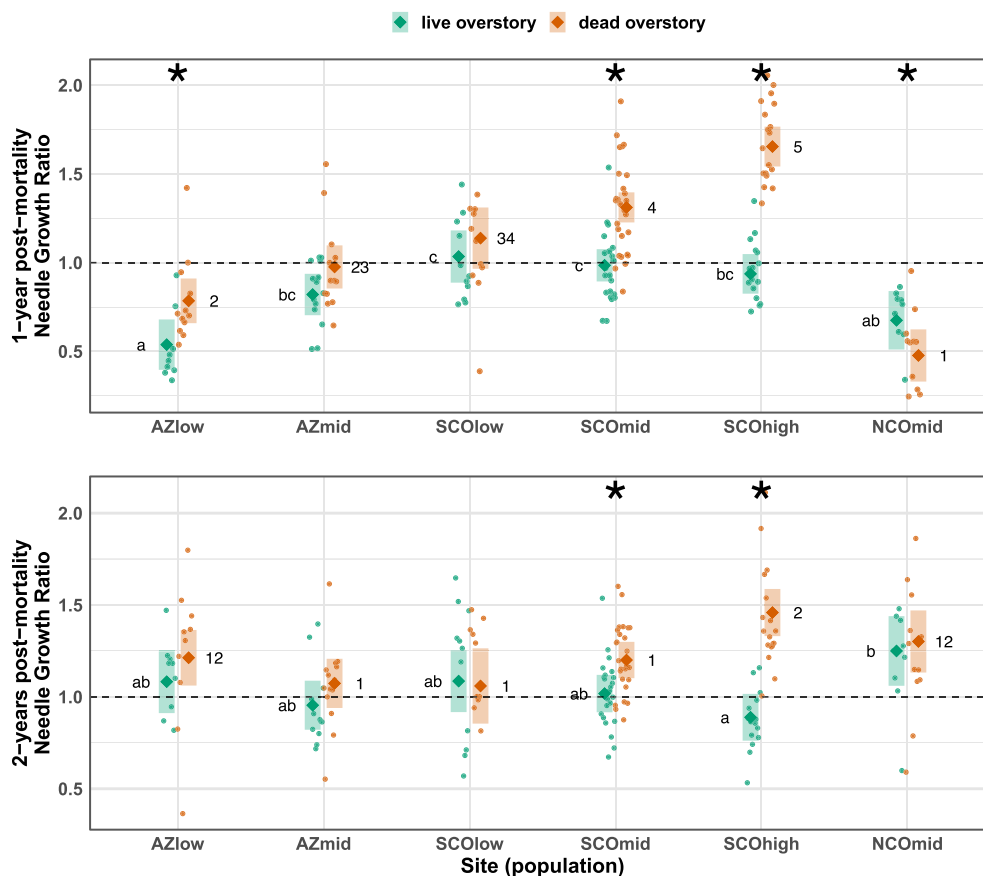


FIGURE 6 Needle growth ratios for the first (i.e. 2021; top panel) and second year (i.e. 2022; bottom panel) of growth following overstorey mortality across all sites, showing model results for the interaction of Site and overstorey treatment (live and dead). Points are tree-level observations; modelled effects are shown with means (large diamond symbols) and 95% confidence intervals (shaded bars around large diamonds). Colours signify live (green) and dead (orange) overstorey treatments. Significance of pairwise comparisons of needle growth ratios between dead and live overstorey treatments within each site is denoted with an asterisk at the top of each plot. Post hoc comparisons of live overstorey treatments across sites and dead overstorey treatments across sites are denoted with letters and numbers, respectively, where shared values suggest no differences. The dashed horizontal line at 1.0 indicates a needle growth ratio value where post-mortality growth is equal to the mean of prior growth years.

3.2.2 | Needle growth following overstorey mortality in relation to post-mortality weather (b)

Needle growth ratios in dead overstorey treatments had a negative relationship with same-year dCMD in both years of measured growth following overstorey treatments, such that growth ratios were lower with weather that was hotter and drier relative to average conditions (Figure 7). This relationship was acute in the first year following overstorey mortality (2021) but much less pronounced in the second year (2022) when dCMDs were close to and below average. While growth ratios in live overstorey treatments were also negatively related to hotter and drier conditions in the first year after overstorey mortality, there was a slight positive relationship in live overstorey treatments in the second year, reflecting increased growth ratios at sites other than SCOhigh and SCOMid. No significant relationships between needle growth ratios and juvenile tree DRC or plot BA were observed in post-mortality weather models.

4 | DISCUSSION

Although patterns of tree mortality and subsequent regeneration failures are well-documented in dryland forest and woodland systems, less is known about direct impacts of overstorey mortality on extant juvenile tree responses. In this study, we found mixed support for our hypothesized trends in juvenile piñon branch and needle growth following an overstorey mortality event that we simulated

through girdling treatments: (1) as hypothesized, positive growth responses following overstorey mortality were consistently evident only at cooler and wetter sites, (2) favourable weather supported positive growth responses following overstorey mortality, but we did not observe patterns of limited growth in dead overstorey plots compared with live overstorey with warmer and drier weather, and (3) we found no evidence for positive growth trends with juvenile tree size.

These results exemplify the predominant role of physiographic (regional, elevational) and corresponding abiotic gradients (Table S1) driving resource availability for tree productivity in these systems (Romme et al., 2009; Shriver et al., 2022). Distinctly strong responses at mid- and high-elevation southern Colorado sites reflect the interplay of favourable abiotic conditions and release from resource competition with previously live overstorey trees, illustrating the role of local structural conditions in mediating post-drought mortality trajectories (Rigling et al., 2013; Vilà-Cabrera et al., 2013). By contrast, the overall lack of growth differences between live and dead overstorey treatments across drier sites suggests that neither facilitative nor competitive interactions between overstorey trees and juvenile growth were dominant under our observed growing conditions (Ploughe et al., 2019). Ultimately, our findings suggest a narrow environmental context, both spatial (more productive sites) and temporal (favourable weather periods), where juvenile piñon pine recruitment may be promoted following overstorey mortality, but also suggest greater vulnerabilities for more arid populations with continuing climate change (Shriver et al., 2022; Zhang et al., 2024).

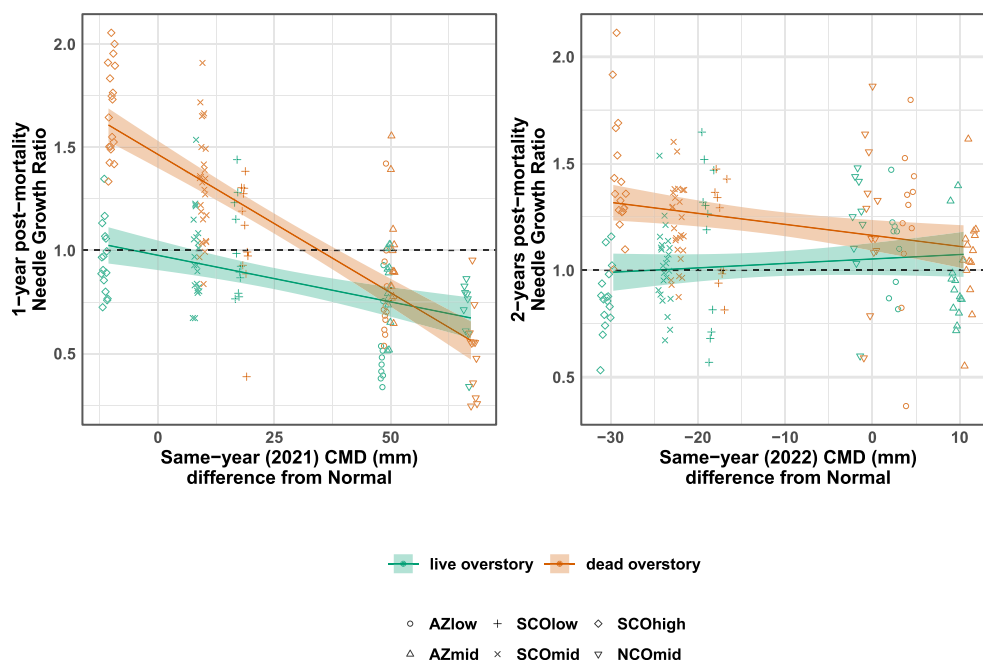


FIGURE 7 Relationship between needle growth ratio and post-mortality weather across sites for first- (2021) and second-year (2022) growth following overstorey mortality treatments. For needle growth, we tested the effects of weather in the same year of measured growth. Colours signify live (green) and dead (orange) overstorey treatments. Shapes denote sites: AZlow = circle; AZmid = upward triangle; SCOLow = plus sign; SCOMid = x; SCOhigh = diamond; NCOMid = downward triangle. The dashed horizontal line at 1.0 indicates a needle growth ratio value where post-mortality growth is equal to the mean of prior growth years.

Our observation of consistent positive growth responses only in wetter sites and weather conditions is in line with numerous prior findings of regeneration and mortality trends (Minott & Kolb, 2020; Redmond et al., 2015, 2018) and projected population vulnerabilities (Shriver et al., 2022, 2021; Urza et al., 2020) across site aridity and soil water availability gradients in these systems. Above-ground tree productivity in piñon-juniper woodlands depends strongly on soil water availability (Kannenberg et al., 2024; Reich et al., 2026), and therefore, stronger growth responses at wetter sites in our study reinforce these expectations, across both regional and elevational gradients (Batllori et al., 2020; Dixit et al., 2022; Vasey et al., 2022). Moreover, compared with sites experiencing above-average CMDs (Figures 5 and 7), positive growth responses to overstorey mortality at mid- and high-elevation southern Colorado sites demonstrated that growth releases were contingent on favourable (here, average) weather, where CMDs were approximately 95%–102% of average (Figure 2). Longer-term study and additional replication at the site level may help resolve the sensitivity of these cooler wetter sites to warmer and drier years (e.g. Redmond et al., 2017), but the strong growth responses observed here are consistent with those reported during even brief periods of favourable conditions in water-limited forests and woodlands (Andrews et al., 2020; Grossiord et al., 2017; Kannenberg et al., 2023).

Higher growth in dead overstorey compared with live overstorey treatments at mid- and high elevations in the southern Colorado region also reflects the interplay of abiotic conditions supportive of growth with competitive release from overstorey trees. Mortality of overstorey trees can facilitate increased water availability and nutrient cycling, leading to enhanced growth responses (Facciano et al., 2023; Grossiord, Gessler, et al., 2018; Ramage et al., 2023). Broadly, at the site level, higher overstorey densities at the mid- and high-elevation (compared with low-elevation, for instance) sites in southern Colorado suggest that observed growth trends in dead compared with live overstorey treatments reflect a release from resource competition. This relationship follows the well-established effects of tree density in south-western US semi-arid conifer forests on soil water availability, resource competition and tree growth and reproduction (Belmonte et al., 2022; Flake & Weisberg, 2019; Petrie & Savage, 2022). Results at these more productive sites contrast with those at the relatively dense mid-elevation Arizona and northern Colorado sites, where post-mortality weather was not favourable (e.g. too hot and dry) for growth release. Consequently, given the conditions observed in this study, overstorey-juvenile growth relationships at these drier sites were neither distinctively facilitative nor competitive, underscoring the dynamic nature of tree interactions relative to site-specific stress conditions and the focal time period considered (Ploughe et al., 2019; Sthultz et al., 2007; Urza et al., 2019).

We hypothesized that warmer and drier weather conditions would result in reduced growth in dead overstorey plots compared with live overstorey due to a loss of overstorey buffering abiotic stressors (De Frenne et al., 2021), but growth was mostly unaffected by overstorey mortality at sites that experienced hot and dry post-treatment

weather (AZlow, AZmid and NCOmid). For local populations that persist in climates with chronic heat- and water-related stresses, tree growth may be especially sensitive to seasonal pulses of favourable weather conditions (Grossiord, Sevanto, et al., 2018; Kerr et al., 2025; Vasey et al., 2022), such as our Arizona region which typically receives 40%–45% of annual precipitation during monsoon season (Figure 2; Peltier & Ogle, 2019; Samuels-Crow et al., 2023). Moreover, heat and drought can strongly limit needle length and shoot growth in piñon pine (Adams et al., 2015; Grossiord et al., 2017; Guérin et al., 2018). Therefore, we expect that under weather conditions observed in our study, changes in resource availability following overstorey mortality were not substantial enough to result in observable growth change, either positive or negative. It is likely that more extended periods of adverse weather would limit subsequent growth (Anderegg & Kannenberg, 2025; Fickle et al., 2025), more consistent with first-year growth patterns in drier locations in our study which followed hot and dry weather in 2020. The exception of elevated growth at the low-elevation Arizona site (Figures 4 and 6) may reflect the diversity of local conditions in this species dependent on inter- and intra-site microenvironmental variation (Kraklow et al., 2025; McDowell et al., 2019), although future research should parse this uniqueness with additional site-level replications.

We found wide variation in growth responses across tree sizes, potentially due to unresolved individual tree and microsite characteristics. Young tree seedlings may be carbon-limited and therefore prioritize above-ground growth for improved light capture (e.g. Augustine & Reinhardt, 2019; Pirtel et al., 2021), but are also frequently limited by low resource-use efficiency (Gyenge & Fernández, 2014). Larger trees may be faced with complex partitioning of growth needs (Cabon et al., 2024), potentially including higher numbers of branches or more leaves per branch (Turrión & Bautista, 2025; Williams et al., 1999). Further study would benefit from pairing physiological measurements to growth responses (Reich et al., 2026) and more precise accounting of variation in individual juvenile microenvironmental characteristics, especially light (Sprugel, 2002), soil water availability (Kannenberg et al., 2024; Williams et al., 2018) and soil nitrogen availability (Grossiord, Gessler, et al., 2018; Gyenge & Fernández, 2014).

5 | CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The need for targeted, system-specific management approaches in piñon-juniper woodlands has become increasingly important due to both the relative lack of current frameworks for these systems, the wide range in types of piñon-juniper systems and the present threats of climate change to piñon-juniper persistence, especially in the south-western United States (Noel et al., 2025; Redmond et al., 2023). The clearest application of results in this study stems from the site-level and weather-driven growth trends, illustrating where conservation efforts may have a higher likelihood of success (Noel et al., 2023). In other dry forest systems in the western United

States, recent literature emphasizes reducing tree density and using uneven-aged silvicultural principles for maintaining structural diversity and improving resistance and resilience to future drought (Fulé et al., 2022; Rodman et al., 2025). In sites which are generally cooler and wetter, such as higher elevation sites, *Pinus edulis* juvenile trees may respond favourably to manipulations of tree density for achieving goals of resilience to climate stressors. However, as evidenced by disturbance recovery outcomes in semi-arid forests and woodlands in other regions, careful consideration of management history, site-specific physiographic characteristics and community-wide interactions is necessary for effective efforts (Moreno-Fernández et al., 2026; Phillips et al., 2024). Our results also reflect the critical role of favourable weather windows that can support tree vigour, and therefore, it is critical to consider the timing of density management treatments in adaptive, anticipatory management efforts (Bradford et al., 2018; Noel et al., 2025). In drier sites, efforts to retain a range of multiple life-stages or age groups may provide a foundation for resilience to uncertain outcomes of elevated climate stress (Ma et al., 2023; Phillips et al., 2024). Ultimately, this study provides evidence for possible positive responses of piñon pine trajectories following overstorey mortality, though the narrow spatial and temporal context for these outcomes highlights potential vulnerabilities at more arid sites, and emphasizes the need for continued research that supports adaptive management in these ecosystems.

AUTHOR CONTRIBUTIONS

Edward M. Hill formulated project ideas with input from all authors, and overall project design was done with equal efforts among all authors. Edward M. Hill, Miranda D. Redmond and Troy W. Ocheltree carried out project implementation. Edward M. Hill completed data analysis, writing, reviewing and editing. Miranda D. Redmond, Troy W. Ocheltree, John B. Bradford and Alexandra K. Urza provided critical input to analyses, and manuscript review and editing.

ACKNOWLEDGEMENTS

We are tremendously grateful for all support received throughout this project. In particular, we would like to thank Gwen Wion for broader project management, Taylar Bankston and Locke Stubblefield for their field and laboratory assistance, and Chuck Rhoades for valuable input during progression of the project. This work was funded by the USDA National Institute of Food and Agriculture (Accession No. 1018490), the BYU Charles Redd Center for Western Studies, the Colorado Mountain Club Foundation and the USDA Forest Service Rocky Mountain Research Station. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or US Government determination or policy. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the US Government.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70310>.

DATA AVAILABILITY STATEMENT

Data are available in the Dryad Data Repository: <https://doi.org/10.5061/dryad.hqbzkh1x6> (Hill et al., 2026).

ORCID

Edward M. Hill  <https://orcid.org/0000-0002-4349-1853>

John B. Bradford  <https://orcid.org/0000-0001-9257-6303>

Alexandra K. Urza  <https://orcid.org/0000-0001-9795-6735>

REFERENCES

- Adams, H. D., Collins, A. D., Briggs, S. P., Vennetier, M., Dickman, L. T., Sevanto, S. A., Garcia-Forner, N., Powers, H. H., & McDowell, N. G. (2015). Experimental drought and heat can delay phenological development and reduce foliar and shoot growth in semiarid trees. *Global Change Biology*, 21, 4210–4220. <https://doi.org/10.1111/gcb.13030>
- Anderegg, W. R. L., & Kannenberg, S. A. (2025). Linking physiology to landscape-scale dieback of Utah juniper during an ongoing megadrought. In B. L. Conkling & K. Pandit (Eds.), *Forest Health Monitoring: Evaluation Monitoring project summaries 2023* (Gen. Tech. Rep. WO-105a) (Chapter 9, pp. 75–79). U.S. Department of Agriculture, Forest Service, Washington, DC. <https://doi.org/10.2737/WO-GTR-105a-Chap9>
- Andrews, C. M., D'Amato, A. W., Fraver, S., Palik, B., Battaglia, M. A., & Bradford, J. B. (2020). Low stand density moderates growth declines during hot droughts in semi-arid forests. *Journal of Applied Ecology*, 57, 1089–1102. <https://doi.org/10.1111/1365-2664.13615>
- Augustine, S. P., & Reinhardt, K. (2019). Differences in morphological and physiological plasticity in two species of first-year conifer seedlings exposed to drought result in distinct survivorship patterns. *Tree Physiology*, 39, 1446–1460. <https://doi.org/10.1093/treephys/tpz048>
- Batllo, E., Lloret, F., Aakala, T., Anderegg, W. R. L., Aynekulu, E., Bendixsen, D. P., Bentouati, A., Bigler, C., Burk, C. J., Camarero, J. J., Colangelo, M., Coop, J. D., Fensham, R., Floyd, M. L., Galiano, L., Ganey, J. L., Gonzalez, P., Jacobsen, A. L., Kane, J. M., ... Zeeman, B. (2020). Forest and woodland replacement patterns following drought-related mortality. *Proceedings. National Academy of Sciences. United States of America*, 117, 29720–29729. <https://doi.org/10.1073/pnas.2002314117>
- Belmonte, A., Sankey, T. T., Biederman, J., Bradford, J. B., & Kolb, T. (2022). Soil moisture response to seasonal drought conditions and post-thinning forest structure. *Ecohydrology*, 15, e2406. <https://doi.org/10.1002/eco.2406>
- Boyden, S. B., Reich, P. B., Puettmann, K. J., & Baker, T. R. (2009). Effects of density and ontogeny on size and growth ranks of three competing tree species. *Journal of Ecology*, 97, 277–288. <https://doi.org/10.1111/j.1365-2745.2008.01477.x>
- Bradford, J. B., Betancourt, J. L., Butterfield, B. J., Munson, S. M., & Wood, T. E. (2018). Anticipatory natural resource science and management for a changing future. *Frontiers in Ecology and the Environment*, 16, 295–303. <https://doi.org/10.1002/fee.1806>
- Bradford, J. B., Schlaepfer, D. R., Lauenroth, W. K., & Palmquist, K. A. (2020). Robust ecological drought projections for drylands in the 21st century. *Global Change Biology*, 26, 3906–3919. <https://doi.org/10.1111/gcb.15075>

- Brodribb, T. J., Powers, J., Cochard, H., & Choat, B. (2020). Hanging by a thread? Forests and drought. *Science*, 368, 261–266. <https://doi.org/10.1126/science.aat7631>
- Cabon, A. (2026). Distal to proximal: A continuum of drivers shaping tree growth and carbon partitioning. *New Phytologist*, 249, 729–735. <https://doi.org/10.1111/nph.70516>
- Cabon, A., Ameztegui, A., Anderegg, W. R. L., Martínez-Vilalta, J., & De Cáceres, M. (2024). Probing the interplay of biophysical constraints and photosynthesis to model tree growth. *Agricultural and Forest Meteorology*, 345, 109852. <https://doi.org/10.1016/j.agrformet.2023.109852>
- Cabon, A., DeRose, R. J., Shaw, J. D., & Anderegg, W. R. L. (2023). Declining tree growth resilience mediates subsequent forest mortality in the US Mountain West. *Global Change Biology*, 29, 4826–4841. <https://doi.org/10.1111/gcb.16826>
- Camarero, J. J. (2021). The drought–dieback–death conundrum in trees and forests. *Plant Ecology and Diversity*, 14, 1–12. <https://doi.org/10.1080/17550874.2021.1961172>
- Camarero, J. J., Pizarro, M., Gernandt, D. S., & Gazol, A. (2024). Smaller conifers are more resilient to drought. *Agricultural and Forest Meteorology*, 350, 109993. <https://doi.org/10.1016/j.agrformet.2024.109993>
- Candido-Ribeiro, R., & Aitken, S. N. (2024). Weak local adaptation to drought in seedlings of a widespread conifer. *New Phytologist*, 241, 2395–2409. <https://doi.org/10.1111/nph.19543>
- Cole, K. L., Shaw, J., Cannella, J., & Ironside, K. E. (2011). Range Map of Colorado Pinyon Pine (*Pinus edulis*) (ed. 2) [WWW Document]. <https://databasin.org/datasets/70ab4ca530864785b7346f82354fd202/>
- Costanza, J. K., Koch, F. H., & Reeves, M. C. (2023). Future exposure of forest ecosystems to multi-year drought in the United States. *Ecosphere*, 14, e4525. <https://doi.org/10.1002/ecs2.4525>
- De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., Ashcroft, M. B., Christiansen, D. M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klimes, D. H., Koelemeijer, I. A., Lembrechts, J. J., Marrec, R., ... Hylander, K. (2021). Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology*, 27, 2279–2297. <https://doi.org/10.1111/gcb.15569>
- Dixit, A., Kolb, T., & Burney, O. (2022). Trade-off between growth rate and water use efficiency in southwestern ponderosa pine provenances. *Forest Ecology and Management*, 515, 120239. <https://doi.org/10.1016/j.foreco.2022.120239>
- Dobrowski, S. Z., Swanson, A. K., Abatzoglou, J. T., Holden, Z. A., Safford, H. D., Schwartz, M. K., & Gavin, D. G. (2015). Forest structure and species traits mediate projected recruitment declines in western US tree species: Tree recruitment patterns in the western US. *Global Ecology and Biogeography*, 24, 917–927. <https://doi.org/10.1111/geb.12302>
- Facciano, L., Sasal, Y., & Suarez, M. L. (2023). How do understorey trees deal with small canopy openings? The case of release in growth following drought-induced tree mortality. *Forest Ecology and Management*, 529, 120692. <https://doi.org/10.1016/j.foreco.2022.120692>
- Falco, G., & Waring, K. M. (2020). Community classification of Piñon-Juniper vegetation in the four corners region, USA. *Forest Science*, 66, 687–699. <https://doi.org/10.1093/forsci/fxaa024>
- Férriz, M., Martín-Benito, D., Cañellas, I., & Gea-Izquierdo, G. (2021). Sensitivity to water stress drives differential decline and mortality dynamics of three co-occurring conifers with different drought tolerance. *Forest Ecology and Management*, 486, 118964. <https://doi.org/10.1016/j.foreco.2021.118964>
- Fickle, J. C., Vargas, G. G., & Anderegg, W. R. L. (2025). Ring-specific vulnerability to embolism reveals accumulation of damage in the xylem. *New Phytologist*, 246, 2046–2058. <https://doi.org/10.1111/nph.70137>
- Flake, S. W., & Weisberg, P. J. (2019). Fine-scale stand structure mediates drought-induced tree mortality in piñon-juniper woodlands. *Ecological Applications*, 29, e01831. <https://doi.org/10.1002/eap.1831>
- Forrester, D. I., Limousin, J.-M., & Pfautsch, S. (2022). The relationship between tree size and tree water-use: Is competition for water size-symmetric or size-asymmetric? *Tree Physiology*, 42, tpac018. <https://doi.org/10.1093/treephys/tpac018>
- Fulé, P. Z., Sánchez Meador, A. J., Moore, M. M., Covington, W. W., Kolb, T. E., Huffman, D. W., Normandin, D. P., & Roccaforte, J. P. (2022). Forest restoration treatments increased growth and did not change survival of ponderosa pines in severe drought, Arizona. *Ecological Applications*, 32, e2717. <https://doi.org/10.1002/eap.2717>
- Gazol, A., Fajardo, A., & Camarero, J. J. (2023). Contributions of intraspecific variation to drought tolerance in trees. *Current Forestry Reports*, 9, 461–472. <https://doi.org/10.1007/s40725-023-00199-w>
- Grams, T. E. E., & Andersen, C. P. (2007). Competition for resources in trees: Physiological versus morphological plasticity. In K. Esser, U. Löttge, W. Beyschlag, & J. Murata (Eds.), *Progress in botany* (pp. 356–381). Springer. https://doi.org/10.1007/978-3-540-36832-8_16
- Grossiord, C., Gessler, A., Reed, S. C., Borrego, I., Collins, A. D., Dickman, L. T., Ryan, M., Schönbeck, L., Sevanto, S., Vilagrosa, A., & McDowell, N. G. (2018). Reductions in tree performance during hotter droughts are mitigated by shifts in nitrogen cycling. *Plant, Cell & Environment*, 41, 2627–2637. <https://doi.org/10.1111/pce.13389>
- Grossiord, C., Sevanto, S., Adams, H. D., Collins, A. D., Dickman, L. T., McBranch, N., Michaletz, S. T., Stockton, E. A., Vigil, M., & McDowell, N. G. (2017). Precipitation, not air temperature, drives functional responses of trees in semi-arid ecosystems. *Journal of Ecology*, 105, 163–175. <https://doi.org/10.1111/1365-2745.12662>
- Grossiord, C., Sevanto, S., Limousin, J.-M., Meir, P., Mencuccini, M., Pangle, R. E., Pockman, W. T., Salmon, Y., Zweifel, R., & McDowell, N. G. (2018). Manipulative experiments demonstrate how long-term soil moisture changes alter controls of plant water use. *Environmental and Experimental Botany, Experiments with Trees: From Seedlings to Ecosystems*, 152, 19–27. <https://doi.org/10.1016/j.jenvexpbot.2017.12.010>
- Guérin, M., Martín-Benito, D., von Arx, G., Andreu-Hayles, L., Griffin, K. L., Hamdan, R., McDowell, N. G., Muscarella, R., Pockman, W., & Gentine, P. (2018). Interannual variations in needle and sapwood traits of *Pinus edulis* branches under an experimental drought. *Ecology and Evolution*, 8, 1655–1672. <https://doi.org/10.1002/ece3.3743>
- Guérin, M., von Arx, G., Martín-Benito, D., Andreu-Hayles, L., Griffin, K. L., McDowell, N. G., Pockman, W., & Gentine, P. (2020). Distinct xylem responses to acute vs prolonged drought in pine trees. *Tree Physiology*, 40, 605–620. <https://doi.org/10.1093/treephys/tpz144>
- Gyenge, J., & Fernández, M. E. (2014). Patterns of resource use efficiency in relation to intra-specific competition, size of the trees and resource availability in ponderosa pine. *Forest Ecology and Management*, 312, 231–238. <https://doi.org/10.1016/j.foreco.2013.09.052>
- Hammond, W. M., Williams, A. P., Abatzoglou, J. T., Adams, H. D., Klein, T., López, R., Sáenz-Romero, C., Hartmann, H., Breshears, D. D., & Allen, C. D. (2022). Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. *Nature Communications*, 13, 1761. <https://doi.org/10.1038/s41467-022-29289-2>
- Hill, E. M., Ocheltree, T., Bradford, J., Urza, A., & Redmond, M. (2026). Overstorey mortality promotes juvenile piñon pine growth during favourable weather at cooler, wetter sites. *Dryad Data Repository*. <https://doi.org/10.5061/dryad.hqbzkh1x6>
- Hover, A., Buissart, F., Caraglio, Y., Heinz, C., Pailler, F., Ramel, M., Vennetier, M., Prévosto, B., & Sabatier, S. (2017). Growth phenology in *Pinus halepensis* Mill.: Apical shoot bud content and shoot elongation. *Annals of Forest Science*, 74, 1–10. <https://doi.org/10.1007/s13595-017-0637-y>
- Isik, K. (1990). Seasonal course of height and needle growth in *Pinus nigra* grown in summer-dry Central Anatolia. *Forest Ecology and Management*, 35, 261–270. [https://doi.org/10.1016/0378-1127\(90\)90007-X](https://doi.org/10.1016/0378-1127(90)90007-X)

- Kannenbergh, S. A., Anderegg, W. R. L., Barnes, M. L., Dannenberg, M. P., & Knapp, A. K. (2024). Dominant role of soil moisture in mediating carbon and water fluxes in dryland ecosystems. *Nature Geoscience*, 17, 38–43. <https://doi.org/10.1038/s41561-023-01351-8>
- Kannenbergh, S. A., Barnes, M. L., Bowling, D. R., Driscoll, A. W., Guo, J. S., & Anderegg, W. R. L. (2023). Quantifying the drivers of ecosystem fluxes and water potential across the soil-plant-atmosphere continuum in an arid woodland. *Agricultural and Forest Meteorology*, 329, 109269. <https://doi.org/10.1016/j.agrformet.2022.109269>
- Kerr, K. L., Anderegg, L. D. L., Trugman, A. T., & Anderegg, W. R. L. (2025). Betting on rains that do not come: Monsoon failure and leaf area overshoot relate to increased tree mortality from drought. *Functional Ecology*, 39, 1840–1852. <https://doi.org/10.1111/1365-2435.70054>
- Kraklow, V., Dickman, L. T., Ryan, M. G., Lathrop, E., Heneghan, J., Musa, D., & Sevanto, S. (2025). Increased water availability at various timescales has different effects on stomatal closure point in isohydric piñon pine and anisohydric juniper. *Scientific Reports*, 15, 16476. <https://doi.org/10.1038/s41598-025-00582-6>
- Lenth, R. V. (2023). emmeans: Estimated marginal means, aka least-squares means.
- Looney, C. E., D'Amato, A. W., Fraver, S., Palik, B. J., & Reinikainen, M. R. (2016). Examining the influences of tree-to-tree competition and climate on size-growth relationships in hydric, multi-aged *Fraxinus nigra* stands. *Forest Ecology and Management*, 375, 238–248. <https://doi.org/10.1016/j.foreco.2016.05.050>
- Ma, Q., Su, Y., Niu, C., Ma, Q., Hu, T., Luo, X., Tai, X., Qiu, T., Zhang, Y., Bales, R. C., Liu, L., Kelly, M., & Guo, Q. (2023). Tree mortality during long-term droughts is lower in structurally complex forest stands. *Nature Communications*, 14, 7467. <https://doi.org/10.1038/s41467-023-43083-8>
- Magnin, A., Torres, C. D., Villalba, R., & Puntieri, J. G. (2017). Does water availability regulate biomass partitioning between trunk and branches? *Plant Biology (Stuttgart, Germany)*, 19, 917–925.
- McBranch, N. A., Grossiord, C., Adams, H., Borrego, I., Collins, A. D., Dickman, T., Ryan, M., Sevanto, S., & McDowell, N. G. (2019). Lack of acclimation of leaf area: Sapwood area ratios in piñon pine and juniper in response to precipitation reduction and warming. *Tree Physiology*, 39, 135–142. <https://doi.org/10.1093/treephys/tpy066>
- McDowell, N. G., Grossiord, C., Adams, H. D., Pinzón-Navarro, S., Mackay, D. S., Breshears, D. D., Allen, C. D., Borrego, I., Dickman, L. T., Collins, A., Gaylord, M., McBranch, N., Pockman, W. T., Vilagrosa, A., Aukema, B., Goodsman, D., & Xu, C. (2019). Mechanisms of a coniferous woodland persistence under drought and heat. *Environmental Research Letters*, 14, 045014. <https://doi.org/10.1088/1748-9326/ab0921>
- Minott, J. A., & Kolb, T. E. (2020). Regeneration patterns reveal contraction of ponderosa forests and little upward migration of pinyon-juniper woodlands. *Forest Ecology and Management*, 458, 117640. <https://doi.org/10.1016/j.foreco.2019.117640>
- Moreno-Fernández, D., del Río, M., Ruiz-Peinado, R., & Cañellas, I. (2026). Summer aridity modulates tree growth response to thinning in Mediterranean pines. *Forest Ecology and Management*, 603, 123485. <https://doi.org/10.1016/j.foreco.2025.123485>
- Noel, A., Schlaepfer, D. R., Barrett, I. P., Duniway, M. C., Norris, J., Domschke, C. T., Butterfield, B. J., Swan, M. C., Hartwig, K., Crist, M. R., & Bradford, J. B. (2025). Shifts in suitability of pinyon-juniper communities: A climate adaptation framework for range-wide management of arid woodland resources. *Forest Ecology and Management*, 596, 123075. <https://doi.org/10.1016/j.foreco.2025.123075>
- Noel, A. R., Shriver, R. K., Crausbay, S. D., & Bradford, J. B. (2023). Where can managers effectively resist climate-driven ecological transformation in pinyon-juniper woodlands of the US southwest? *Global Change Biology*, 29, 4327–4341. <https://doi.org/10.1111/gcb.16756>
- Peltier, D. M. P., & Ogle, K. (2019). Legacies of La Niña: North American monsoon can rescue trees from winter drought. *Global Change Biology*, 25, 121–133. <https://doi.org/10.1111/gcb.14487>
- Petrie, M., & Savage, N. (2022). Climate and landscape variation shapes the water balance of piñon pine-juniper woodlands. *Agricultural and Forest Meteorology*, 323, 109068. <https://doi.org/10.1016/j.agrformet.2022.109068>
- Phillips, M. L., Lauria, C., Spector, T., Bradford, J. B., Gehring, C., Osborne, B. B., Howell, A., Grote, E. E., Rondeau, R. J., Trimber, G. M., Robinson, B., & Reed, S. C. (2024). Trajectories and tipping points of piñon-juniper woodlands after fire and thinning. *Global Change Biology*, 30, e17149. <https://doi.org/10.1111/gcb.17149>
- Pirtel, N. L., Hubbard, R. M., Bradford, J. B., Kolb, T. E., Litvak, M. E., Abella, S. R., Porter, S. L., & Petrie, M. D. (2021). The aboveground and belowground growth characteristics of juvenile conifers in the southwestern United States. *Ecosphere*, 12, e03839. <https://doi.org/10.1002/ecs2.3839>
- Ploughe, L. W., Jacobs, E. M., Frank, G. S., Greenler, S. M., Smith, M. D., & Dukes, J. S. (2019). Community response to extreme drought (CRED): A framework for drought-induced shifts in plant-plant interactions. *New Phytologist*, 222, 52–69. <https://doi.org/10.1111/nph.15595>
- R Core Team. (2023). *R: A language and environment for statistical computing*.
- Ramage, B. S., Johnson, D. J., & Chan, D. M. (2023). Effects of drought, disturbance, and biotic neighborhood on experimental tree seedling performance. *Ecology and Evolution*, 13, e10413. <https://doi.org/10.1002/ece3.10413>
- Redmond, M. D., & Barger, N. N. (2013). Tree regeneration following drought- and insect-induced mortality in piñon-juniper woodlands. *The New Phytologist*, 200, 402–412. <https://doi.org/10.1111/nph.12366>
- Redmond, M. D., Cobb, N. S., Clifford, M. J., & Barger, N. N. (2015). Woodland recovery following drought-induced tree mortality across an environmental stress gradient. *Global Change Biology*, 21, 3685–3695. <https://doi.org/10.1111/gcb.12976>
- Redmond, M. D., Kelsey, K. C., Urza, A. K., & Barger, N. N. (2017). Interacting effects of climate and landscape physiography on piñon pine growth using an individual-based approach. *Ecosphere*, 8, e01681. <https://doi.org/10.1002/ecs2.1681>
- Redmond, M. D., Urza, A. K., & Weisberg, P. J. (2023). Managing for ecological resilience of pinyon-juniper ecosystems during an era of woodland contraction. *Ecosphere*, 14, e4505. <https://doi.org/10.1002/ecs2.4505>
- Redmond, M. D., Weisberg, P. J., Cobb, N. S., & Clifford, M. J. (2018). Woodland resilience to regional drought: Dominant controls on tree regeneration following overstorey mortality. *Journal of Ecology*, 106, 625–639. <https://doi.org/10.1111/1365-2745.12880>
- Reich, E. G., Samuels-Crow, K., Bradford, J. B., Litvak, M., Schlaepfer, D. R., & Ogle, K. (2026). Beyond optimality: Dryland ecosystems infrequently use water efficiently for carbon gain. *Agricultural and Forest Meteorology*, 378, 110996. <https://doi.org/10.1016/j.agrformet.2025.110996>
- Rigling, A., Bigler, C., Eilmann, B., Feldmeyer-Christe, E., Gimmi, U., Ginzler, C., Graf, U., Mayer, P., Vacchiano, G., Weber, P., Wohlgemuth, T., Zweifel, R., & Dobbertin, M. (2013). Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. *Global Change Biology*, 19, 229–240. <https://doi.org/10.1111/gcb.12038>
- Rodman, K. C., Bradford, J. B., Formanack, A. M., Fulé, P. Z., Huffman, D. W., Kolb, T. E., Miller-ter Kuile, A. T., Normandin, D. P., Ogle, K., Pedersen, R. J., Schlaepfer, D. R., Stoddard, M. T., & Waltz, A. E. M. (2025). Restoration treatments enhance tree growth and alter climatic constraints during extreme drought. *Ecological Applications*, 35, e3072. <https://doi.org/10.1002/eap.3072>
- Romme, W. H., Allen, C. D., Bailey, J. D., Baker, W. L., Bestelmeyer, B. T., Brown, P. M., Eisenhart, K. S., Floyd, M. L., Huffman, D. W., & Jacobs, B. F. (2009). Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon-juniper vegetation of the western United States. *Rangeland Ecology & Management*, 62, 203–222.

- Rother, M. T., Veblen, T. T., & Furman, L. G. (2015). A field experiment informs expected patterns of conifer regeneration after disturbance under changing climate conditions. *Canadian Journal of Forest Research*, 45, 1607–1616. <https://doi.org/10.1139/cjfr-2015-0033>
- Samuels-Crow, K. E., Peltier, D. M. P., Liu, Y., Guo, J. S., Welker, J. M., Anderegg, W. R. L., Koch, G. W., Schwalm, C., Litvak, M., Shaw, J. D., & Ogle, K. (2023). The importance of monsoon precipitation for foundation tree species across the semiarid southwestern U.S. *Frontiers in Forests and Global Change*, 6, 1116786. <https://doi.org/10.3389/ffgc.2023.1116786>
- Schiestl-Aalto, P., & Mäkelä, A. (2017). Temperature dependence of needle and shoot elongation before bud break in Scots pine. *Tree Physiology*, 37, 316–325. <https://doi.org/10.1093/treephys/tpw120>
- Seidel, H., Matiu, M., & Menzel, A. (2019). Compensatory growth of scots pine seedlings mitigates impacts of multiple droughts within and across years. *Frontiers in Plant Science*, 10, 519. <https://doi.org/10.3389/fpls.2019.00519>
- Shriver, R. K., Yackulic, C. B., Bell, D. M., & Bradford, J. B. (2021). Quantifying the demographic vulnerabilities of dry woodlands to climate and competition using rangewide monitoring data. *Ecology*, 102, e03425. <https://doi.org/10.1002/ecy.3425>
- Shriver, R. K., Yackulic, C. B., Bell, D. M., & Bradford, J. B. (2022). Dry forest decline is driven by both declining recruitment and increasing mortality in response to warm, dry conditions. *Global Ecology and Biogeography*, 31, 2259–2269. <https://doi.org/10.1111/geb.13582>
- Sprugel, D. G. (2002). When branch autonomy fails: Milton's law of resource availability and allocation. *Tree Physiology*, 22, 1119–1124. <https://doi.org/10.1093/treephys/22.15-16.1119>
- Stultz, C. M., Gehring, C. A., & Whitham, T. G. (2007). Shifts from competition to facilitation between a foundation tree and a pioneer shrub across spatial and temporal scales in a semiarid woodland. *New Phytologist*, 173, 135–145. <https://doi.org/10.1111/j.1469-8137.2006.01915.x>
- Turrión, D., & Bautista, S. (2025). Tree-architectural response to restoration thinning pattern in post-fire Aleppo pine forests—A modular view of tree plasticity. *Forest Ecology and Management*, 595, 123025. <https://doi.org/10.1016/j.foreco.2025.123025>
- Urza, A. K., Weisberg, P. J., Chambers, J. C., & Sullivan, B. W. (2019). Shrub facilitation of tree establishment varies with ontogenetic stage across environmental gradients. *New Phytologist*, 223, 1795–1808. <https://doi.org/10.1111/nph.15957>
- Urza, A. K., Weisberg, P. J., & Dilts, T. (2020). Evidence of widespread topoclimatic limitation for lower treelines of the Intermountain West, United States. *Ecological Applications*, 30, e02158. <https://doi.org/10.1002/eap.2158>
- Vasey, G. L., Urza, A. K., Chambers, J. C., Pringle, E. G., & Weisberg, P. J. (2023). Clinal variations in seedling traits and responses to water availability correspond to seed-source environmental gradients in a foundational dryland tree species. *Annals of Botany*, 132, mcad041. <https://doi.org/10.1093/aob/mcad041>
- Vasey, G. L., Weisberg, P. J., & Urza, A. K. (2022). Intraspecific trait variation in a dryland tree species corresponds to regional climate gradients. *Journal of Biogeography*, 49, 2309–2320. <https://doi.org/10.1111/jbi.14515>
- Vilà-Cabrera, A., Martínez-vilalta, J., Galiano, L., & Retana, J. (2013). Patterns of Forest decline and regeneration across Scots pine populations. *Ecosystems*, 16, 323–335. <https://doi.org/10.1007/s10021-012-9615-2>
- Wang, T., Hamann, A., Spittlehouse, D., & Carroll, C. (2016). Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS One*, 11, e0156720.
- Williams, C. J., Snyder, K. A., & Pierson, F. B. (2018). Spatial and temporal variability of the impacts of pinyon and juniper reduction on hydrologic and erosion processes across climatic gradients in the western US: A regional synthesis. *Water*, 10, 1607.
- Williams, H., Messier, C., & Kneeshaw, D. D. (1999). Effects of light availability and sapling size on the growth and crown morphology of understorey Douglas-fir and lodgepole pine. *Canadian Journal of Forest Research*, 29, 222–231.
- Xu, C., Liu, H., Ciais, P., Hartmann, H., Camarero, J. J., Wu, X., Hammond, W. M., Allen, C. D., & Chen, F. (2024). Enhanced drought exposure increasingly threatens more forests than observed. *Earth's Future*, 12, e2023EF003705. <https://doi.org/10.1029/2023EF003705>
- Zhang, F., Biederman, J. A., Schlaepfer, D. R., Bradford, J. B., Reed, S. C., & Smith, W. K. (2024). Increasing soil water drought in response to altered precipitation timing across the Western United States. *Ecohydrology*, n/a, e2749. <https://doi.org/10.1002/eco.2749>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Site characteristics, with plot-level averages and variation (± 1 standard deviation) shown where data were available. Total basal area represents all overstorey (≥ 9.0 cm DRC) trees in the 7 m radius plot surrounding each focal tree. Juniper dominance was calculated as the proportion of juniper overstorey basal area relative to other tree species. Soils information includes estimated soil water storage, based on soil physical properties, which is generally described by soil types given in the table. Site details also include climate and study-year weather conditions. Climate information includes 30-year normal precipitation, vapour pressure deficit (VPD), climatic moisture deficit (CMD; Hargreaves) and monsoonality (all data obtained from ClimateNA, <https://climatena.ca/>). Additionally, included yearly differences from 30-year normals for years included in our analyses (2020–2022) which illustrate relative weather-related stresses specific to each site. Site codes: AZlow=low-elevation, northern Arizona; AZmid=middle-elevation, northern Arizona; SCOLow=low-elevation, south-western Colorado; SCOMid=middle-elevation, south-western Colorado; SCOHIGH=high-elevation, south-western Colorado; NCOMid=middle-elevation, northern Colorado.

Table S2. Model results for all models described in analysis. Table information includes model (all sites models, and post-mortality weather models), year of growth modelled (1- and 2-years after overstorey mortality; i.e. 2021 and 2022), and covariates included in each model for branch and needle growth ratios. Model information includes coefficient estimates ('Est.') for each model covariate, in addition to standard errors ('SE') of each estimate, model degrees of freedom ('DF'), 95% bounds of confidence interval estimates ('CI low' and 'CI high'), and model adjusted R^2 .

How to cite this article: Hill, E. M., Ocheltree, T. W., Bradford, J. B., Urza, A. K., & Redmond, M. D. (2026). Overstorey mortality promotes juvenile piñon pine growth during favourable weather at cooler, wetter sites. *Journal of Ecology*, 114, e70310. <https://doi.org/10.1111/1365-2745.70310>