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ARTICLE

Climate Ecology

Complex trajectories of tree growth in the southwestern United States after severe drought

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Abstract

Climate change driven extreme droughts have major impacts on forest ecosystems, including large-scale mortality and reduced primary production, which feedback to affect the global carbon cycle. The long-term impacts of extreme drought events on forest mortality, ecosystem responses, and recovery/post-drought trajectories are poorly understood. In this study, we combine annual tree ring widths of five major species occurring in the southwestern United States and data obtained from long-term forest inventory and monitoring plots to study the effect of an extreme drought event in 2002 on subsequent tree growth. We quantified the extent to which trees that survived the drought had increased growth due to potential increases in resources from reduced stand density or reduced growth due to lingering impacts of drought stress. We found diverse patterns of post-drought growth trajectories across species, with drastic increases in growth in some species such as trembling aspen (*Populus tremuloides*) and clear growth suppression in other species such as ponderosa pine (*Pinus ponderosa*), reflecting notable drought legacy effects. Total basal area was the best predictor of post-drought growth responses, though the regression effect (positive or negative) varied by species; for example, ponderosa pine showed less growth than predicted in higher density stands while spruce had greater growth than expected in the higher density stands. Climatic water deficit and stand age also emerged as important drivers of post-drought growth trajectories for multiple species. The results of this study can help to elucidate how different forest types in the southwestern United States will respond to future drought events and the ramifications for carbon cycling in this region.

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competition, dendrochronology, drought, forest, mortality

INTRODUCTION

The response of forest ecosystems to increasingly frequent extreme climate events will have manifold impacts on biodiversity, ecosystem function and services, and the climate. Climate change is projected to drive an increase in the frequency and severity of droughts in many terrestrial vegetation systems (Intergovernmental Panel on Climate Change, 2021). Severe drought, often exacerbated by elevated temperature and atmospheric dryness, can result in declines in growth, widespread tree die-off (Eamus et al., 2013), and affect forest carbon sinks (Ma et al., 2012; Schwalm et al., 2012; Wigneron et al., 2020; Yang et al., 2018). Drought-induced tree mortality has been observed in a wide diversity of forest types across the globe (Allen et al., 2010; Anderegg, Hicke, et al., 2015; Phillips et al., 2010) and is projected to increase in many places, including the southwestern United States (Buotte et al., 2019). Drought-induced mortality and accompanying disturbances, such as increased insect attack and wildfire, are dramatically altering the carbon cycle (Reyer et al., 2015) and the distribution of ecosystems (Adams et al., 2009; Allen et al., 2015; Klos et al., 2009; Veblen et al., 1991). Our current understanding, however, of the long-term ecological and carbon cycle effects of these mortality events remains uncertain. Thus, more research is needed to determine the long-term effects of extreme drought on forests as well as the dynamics of forest recovery following extreme drought (Martínez-Vilalta et al., 2012).

Forests are a significant contributor to the terrestrial carbon sink (Bonan, 2008; Pan et al., 2011). Terrestrial ecosystems, driven largely by forests, remove approximately 3.1 petagrams of anthropogenic-produced carbon dioxide from the atmosphere annually (Friedlingstein et al., 2022). Some forests are more resilient to changes in carbon uptake rates following disturbance events such as drought (Gough et al., 2013; Reed et al., 2014). Processes underlying long-term changes in vegetation composition—for example, changes in demographic rates such as tree growth following climate-driven disturbances (e.g., drought)—are difficult to accurately represent in vegetation models (Fisher et al., 2018; Kolus et al., 2019). Therefore, improving dynamic global vegetation models (DGVMs) is critical for projecting the strength and direction of carbon fluxes of forests in response to climate change and extreme drought events.

Forest responses to drought depend on a suite of species-specific functional traits that mediate tree growth sensitivity to soil moisture and vapor pressure deficit (VPD) (Flo et al., 2021). Furthermore, competition with other trees is mediated by water availability, which is in turn affected by stand-level processes such as run-off, soil evaporation, transpiration, and groundwater recharge. Disturbances, such as drought, have the ability to affect competition for water by altering resource availability and ecosystem structure (Adams et al., 2012; Black et al., 1980; Morillas et al., 2017; Pickett & White, 1985). In managed forests, thinning, also known as crop tree release, has been frequently used to reduce competition (Bradford et al., 2010). Such thinning can result in increased resistance and resilience to drought (D'Amato et al., 2013; Fiddler et al., 1989; Laurent et al., 2003; Sohn et al., 2016), increased resistance to bark beetle outbreaks (Hood et al., 2016), and sometimes, reduced tree mortality of the remaining trees (McCauley et al., 2022). However, the vast majority of studies have only examined monoculture stands with regular thinning patterns and timelines (Cescatti & Piutti, 1998; Giuggiola et al., 2013; Laurent et al., 2003). Silvicultural management generally causes relatively little damage or stress to surviving trees, while drought-driven mortality events often cause hydraulic damage that can persist for a decade or more even for trees that survive (Anderegg et al., 2013). Thus, it remains to be seen whether increases in resilience and growth in thinned stands are also found following mortality from extreme climate events (e.g., drought), and what factors mediate positive or negative post-drought growth trajectories.

Tree rings provide a powerful tool to track changes in primary productivity through shifts in radial growth, capturing the history of tree growth without the need of repeated forest inventories (Fritts & Swetnam, 1989). Tree rings enable quantification of decreases in radial growth during a drought (Camarero et al., 2018; Gazol et al., 2017, 2020) and changes in radial growth following drought (Huang et al., 2018). Legacy effects can trigger a transient or continued decline in growth even after a return to average precipitation levels when there is significant damage to functional xylem (Anderegg, Schwalm, et al., 2015; Peltier et al., 2016). Since radial growth is strongly related to water availability, particularly in conifers in the southwestern United States, tree ring growth patterns paired with climate data can be used to quantify tree growth responses following drought and a variety of other disturbances (Altman et al., 2016; Bošeľa et al., 2014; Tomita & Hiura, 2024; Yang et al., 2022). Thus, combining tree ring and climate data

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can enable the identification of spatial and temporal relationships between large-scale climatic events, such as drought, and the physiological responses of individual trees, enhancing the ability to predict stand-level growth trends and ecosystem resilience.

To quantify tree growth patterns after a drought disturbance, we analyzed tree ring data in forest plots before and after the severe 2002 drought in the southwestern United States that caused variable mortality across the region (Breshears et al., 2005). We aimed to elucidate the long-term impacts of droughts, including the process of stand recovery, species-specific growth responses, and changes in response and recovery due to climate. We sought to answer the following questions: (1) Did the 2002 drought leave a growth legacy? That is, was there a change in growth post drought compared to growth predicted from post-drought climate and pre-drought growth-climate sensitivity? (2) What factors among broad scale climate variables, species-specific traits, and stand characteristics mediate the magnitude and direction of post-drought tree growth legacies? We hypothesized that observed growth would increase compared to predicted growth for more drought tolerant species due to a reduction in competition for surviving trees, while in less drought tolerant species, increased hydraulic damage during the drought event would hinder surviving trees from taking advantage of improved water availability.

METHODS

Field sites

We focused on 33 US Forest Service Forest Inventory and Analysis (FIA) plots in the southwestern United States (Arizona, Colorado, and Utah) located in pinyon-juniper woodlands dominated by *Pinus edulis* (pinyon) and *Juniperus osteosperma* (juniper), *Pinus ponderosa* (ponderosa) forests, *Picea engelmannii* (spruce) forests, and *Populus tremuloides* (aspen) forests (Figure 1). We selected plots that were established in 2004, for which the FIA program collected survey census data in 2004 and 2014. FIA "Phase 2" permanent plots provide field measurements such as tree size, site information, forest type, disturbances, mortality, and soil characteristics. We used Phase 2 data collected in 2004 to identify FIA plots that recorded mortality at the establishment of plots (Appendix S1: Figure S1). Mortality is recorded as a binary observation of tree death (living or dead). In addition, we used stand age, total basal area (from 2004), and

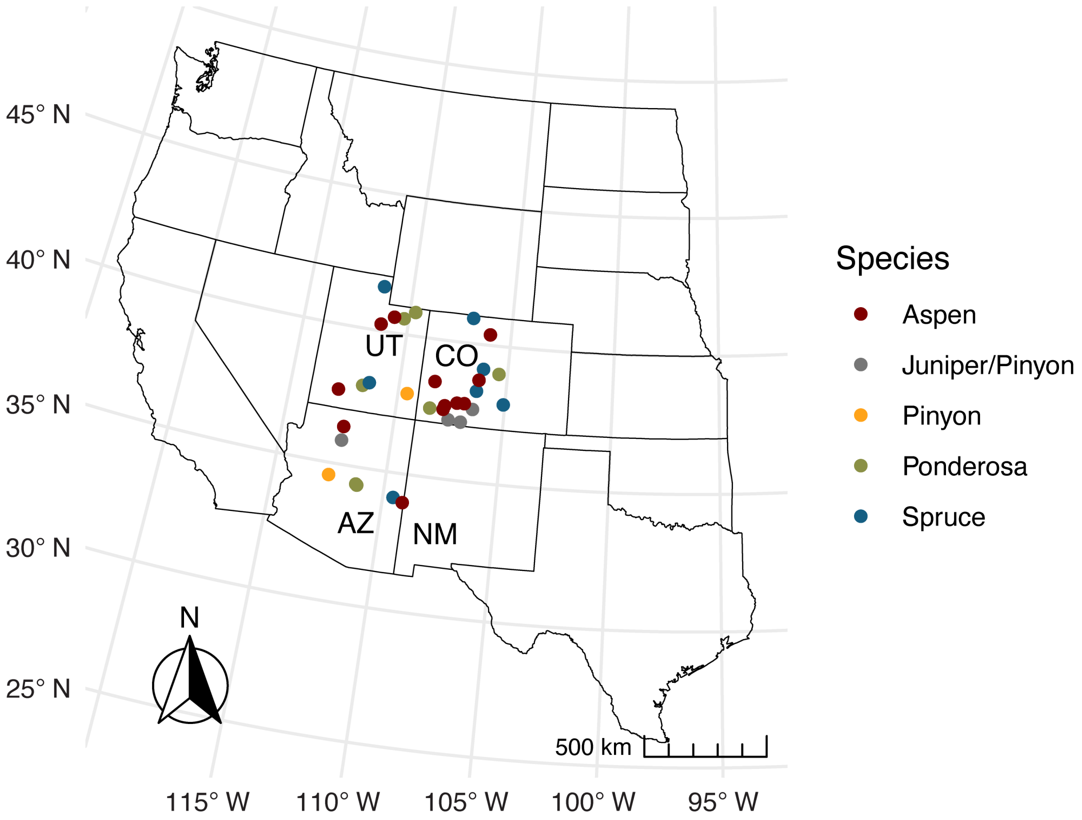

FIGURE 1 Locations of USFS Forest Inventory and Analysis (FIA) plots that this study used, all occurring in the southwestern United States, including states Arizona (AZ), Colorado (CO), and Utah (UT). Colors indicate species cored at each site.

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records of species-specific mortality in each plot to build mixed-effects models to compare measured and expected growth. These data were also used to analyze the percent change in growth for each species at each plot when compared to the species that died (same species, different species, both same and different, or no mortality recorded in the FIA data). There were FIA data and tree core samples collected in New Mexico that also suffered severe drought; however, because these plots were remeasured in 2009, we chose to exclude these sites for consistency with the other sites, which were measured in 2004 and 2014 (Truettner et al., 2018).

Tree ring samples

Considering the nuanced interactions between trees and their environment, particularly in response to climatic disturbances such as drought, it becomes imperative to carefully select and justify the methodologies employed in dendroecological analyses. The use of raw ring width data (RRW) in such analyses can present several advantages, especially when examining post-drought growth responses in trees. RRW provide a direct measure of annual growth, allowing for a more explicit assessment of the magnitude and timing of growth anomalies following drought or disturbance events. This approach enabled us to explore the intricate relationships between climate variability, tree physiology, and ecosystem dynamics without potential signal dampening introduced by standardized indices (Canham et al., 2018). By using RRW data, we can better capture ecological variability in tree growth responses and assess the influence of various environmental factors, such as competition, on growth dynamics. Therefore, in the context of our objectives and the complex nature of post-drought tree growth patterns observed in forests in the southwestern United States, the utilization of RRW data allows us to better assess the average impact of climate conditions on tree growth.

We utilized published tree ring width records from Truettner et al. (2018) for four conifer species, as well as unpublished tree ring width data for aspen, which was collected and processed concurrently with the conifer data, following exactly the same methodologies. All tree ring data were used to quantify radial stem growth in our target plots and can be found on Figshare (Zenes et al., 2025). Details on tree core collection and processing methods, including cross-dating and measurement procedures, are provided in Truettner et al. (2018). No additional cross-dating or measurements were performed for this study. The tree ring width data are publicly available from Figshare (https://doi.org/10.6084/m9.figshare.29901086). All cores were collected in 2014 at each of our four forest type sites. We used these tree ring width records to identify growth patterns and post-drought tree growth. The datasets contain tree cores from 10 mature trees per species from a range of sizes from each plot. We used RRWs for each species in each plot as all trees were mature (i.e., minimal-to-no age signal), and we only used the tree ring measurements from 1960 to 1989 as our baseline. The ring width data were not detrended as this could dampen certain competitive release and climate response signals (Canham et al., 2018), particularly as 2002 and later years are some of the driest on record in the southwestern United States. We verified the lack of a strong age signal by plotting RRW versus time over our study period (1960–1989) (Appendix S1: Figures S2–S6 for an example of each species).

Climate data

We obtained climate data from TerraClim (1/24°, ~4-km high spatial resolution global dataset; Abatzoglou et al., 2018). We used the following annual climate variables: climatic water deficit (in millimeters, CWD), annual maximum temperature (in degrees Celsius, $T_{\max}$), annual precipitation (in millimeters, PPT), snow water equivalent (in millimeters, SWE), VPD (in kilopascals), actual evapotranspiration (in millimeters, AET), soil water content (in millimeters, SWC), and Palmer Drought Severity Index (PDSI). These data were downloaded in April 2020 in netCDF format from: http://thredds.northwestknowledge.net:8080/thredds/terraclimate_aggregated.html. The downloading and processing script are available from Zenodo (Zenes, 2025).

Statistical climate growth models and RRW residuals

We analyzed RRWs (Williams et al., 2010) via linear mixed-effects models relating baseline growth (during 1960–1989) to the aforementioned annual climate variables (CWD, $T_{\max}$, PPT, SWE, VPD, SWC, and PDSI) and all two-way interactions between these variables. We incorporated plot random effects, thus allowing the intercept and all regression coefficients to vary by plot. We used 1960–1989 as a baseline period to train the growth-climate model because these three decades provide a reasonable estimate of long-term climate prior to widespread regional droughts (Williams et al., 2012). We then used model selection criteria of root mean square error (RMSE) and Akaike information criterion (AIC) to determine which combination of climate variables (described above) provided the best fit (smallest AIC) for each species and chose the best fit model over the training 1960–1989 period. We used the r.squaredGLMM function in the MuMIn R

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package (Bartoń, 2024) to calculate the conditional and marginal R^2 values, $R^2{}_c$ and $R^2{}_m$, respectively, for our models (Appendix S1: Table S1). $R^2{}_c$ provides an index of model fit based on all included covariates and the spatial (plot) random effects, whereas $R^2{}_m$ describes model fit in the absence of the plot random effects, thus providing an index of the amount of variation explained by climate variables alone.

To estimate growth legacies of the 2002 drought, we applied the growth-climate model for each species to derive "predicted growth" during the 2000–2014 study years, given the climate reported for those years. The approach follows methods from Anderegg, Schwalm, et al. (2015), which quantified drought legacies by calculating the difference between observed and predicted growth after drought events, based on correlations between tree ring width and climate during pre-drought years. Predicted growth following the 2002 mortality event was then compared with observed growth measured as RRW to determine whether growth sensitivity to climate (Peltier & Ogle, 2020) changed due to the mortality event. The residual RRWs (observed − predicted) were calculated for each tree core (Appendix S1: Figure S7) and binned by species for the 3 years (2003–2005), 5 years (2003–2007), and 10 years (2003–2012) following the 2002 severe drought (Breshears et al., 2005) (Figure 2). Two-sided

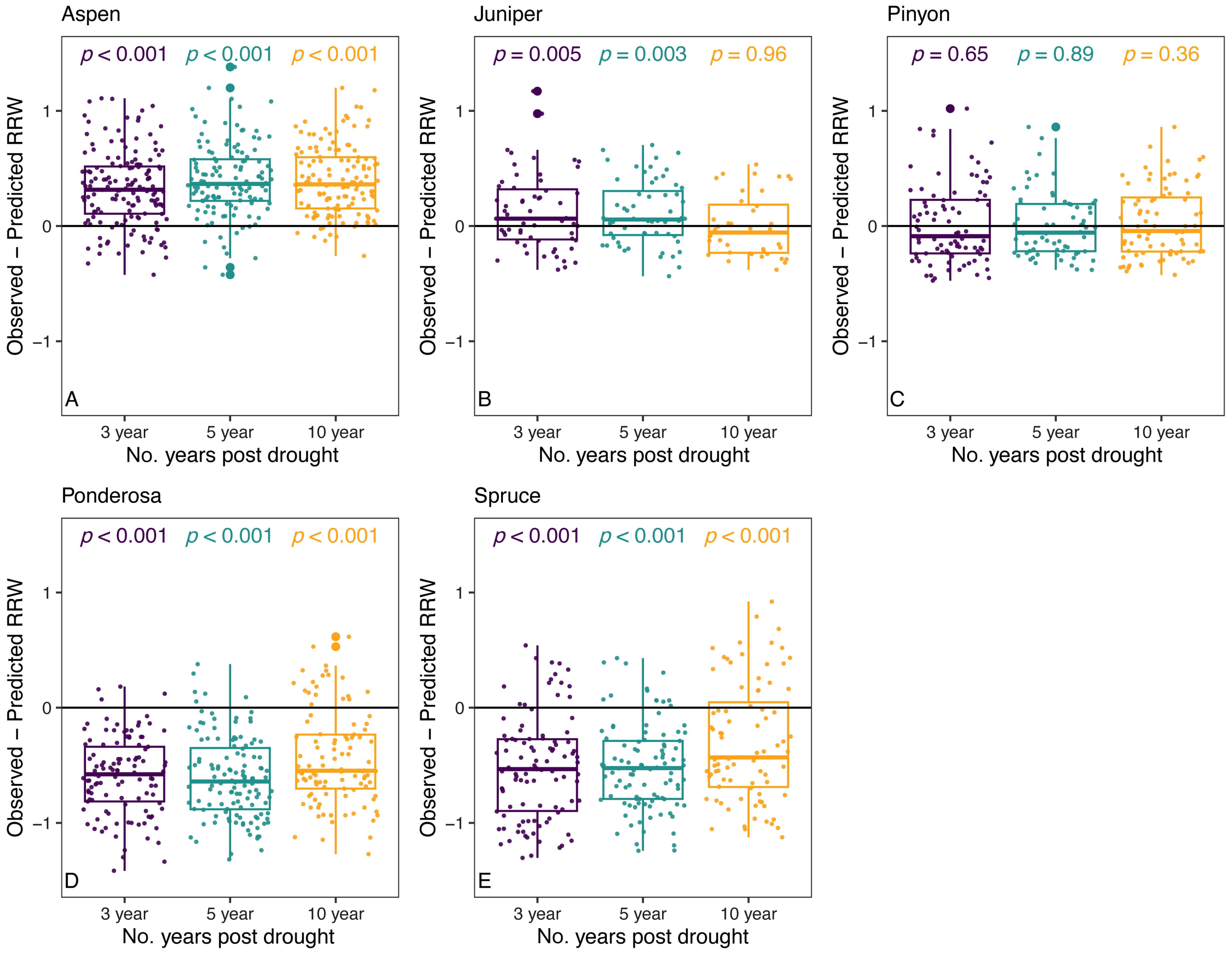

FIGURE 2 Residual (observed − predicted) raw ring widths (RRW, in millimeters) binned across years after the 2002 drought (i.e., 3 years = 2003–2005; 5 years = 2003–2007; 10 years = 2003–2012). The thick horizontal line within each boxplot shows the median residual, and the boxes represent the first and third quartiles. Each point is the RRW residual for a single tree core sample. The horizontal black line is the zero line; residuals greater than zero indicate more growth than predicted (e.g., likely due to competitive release) and residuals less than zero indicate less growth than predicted (e.g., likely due to long-lasting damage). Different panels represent different species: (A) aspen, (B) juniper, (C) pinyon, (D) ponderosa, and (E) spruce; *p*-values above each box plot indicate whether the mean residual is significantly different from zero. The whiskers for each boxplot extend to the furthest data point within 1.5× the interquartile range (IQR) from the third quartile (greater than) or the first quartile (less than).

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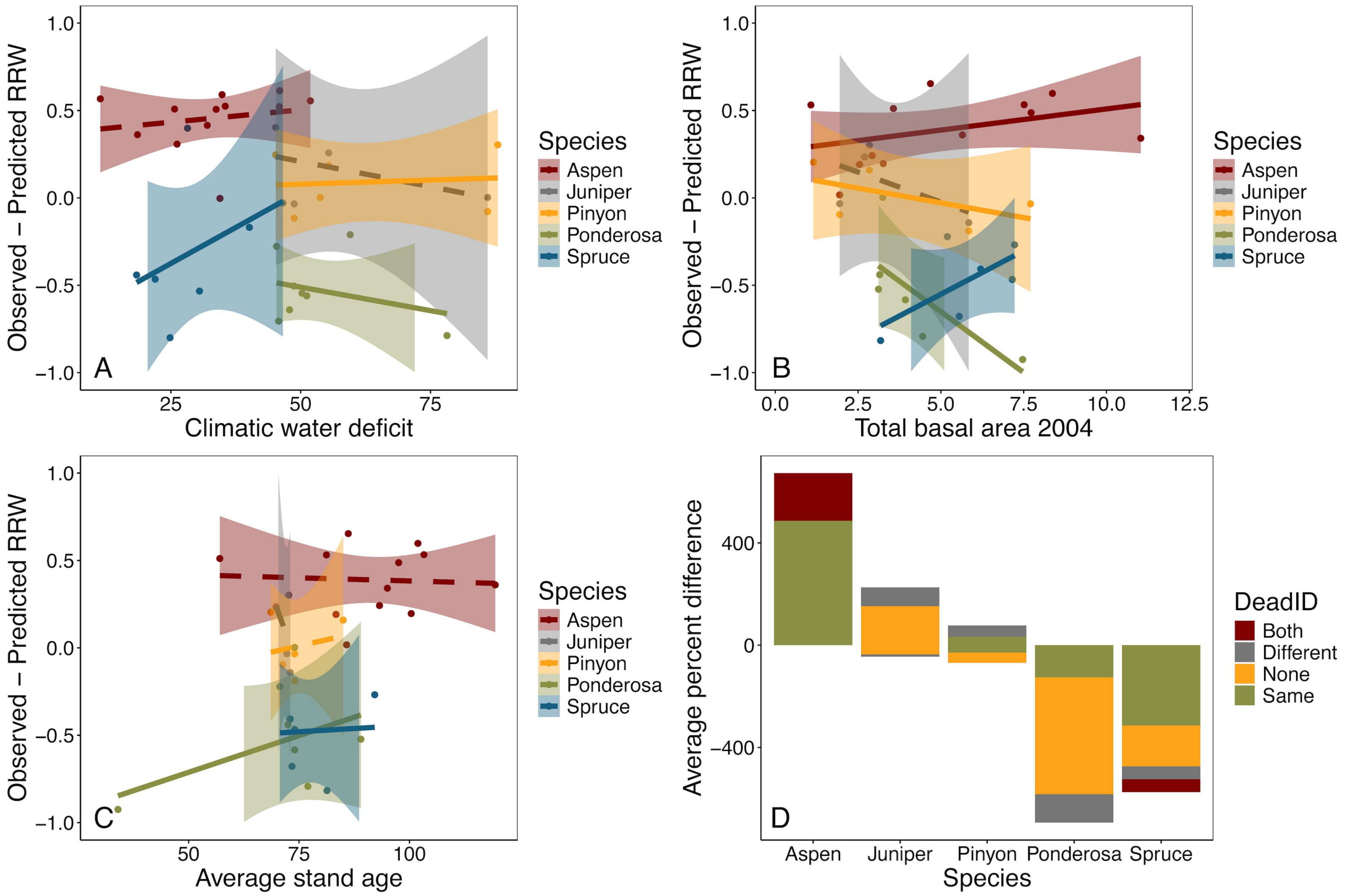

FIGURE 3 Residual (observed − predicted) raw ring width (RRW, in millimeters) for each study plot grouped by species versus (A) the baseline climatic water deficit (in millimeters; 1960–1989), (B) total basal area (in square meters per hectare) measured in each plot in 2004, and (C) the average stand age (in years) measured in 2004 grouped by species. For panels (A)–(C), colored shading represents the 95% CI, solid lines represent significant regressions ($p < 0.05$), and dashed lines represent nonsignificant regressions. (D) Average percent difference in RRW residuals for 5 years post drought (2003–2007) with each bar representing a species and each sub-bar representing a plot. Colors represent the identity of the tree species recorded dead in 2004 in each plot as recorded by Forest Inventory and Analysis (FIA) surveys. DeadID categories are: "Different" when species other than the target species died (e.g., if spruce were recorded dead in an aspen plot), "Same" when the species that died was the same as the target species (e.g., if only aspen were recorded dead in an aspen plot), "Both" when species that died included the target species and other species (e.g., if aspen and spruce were recorded dead in an aspen plot), and "None" if there was no mortality recorded from the FIA surveys.

t tests were used to determine whether the mean residual (i.e., drought-associated prediction error) for each bin significantly differed from 0. In each plot, we also examined the average percent difference in residuals of each species for the 5 years post drought, with reference to the identity of the species that died in the plot as recorded by the FIA surveys (Figure 3D). We assigned one of four categories based on the relationship between dead trees and the cored trees: plots where mortality was limited to the same species as the cored trees (same), plots where mortality was of a different species than the cored trees (different), plots where mortality included both the same species and different species (both), and plots with no mortality (none).

Mixed-effects models to explore post-drought growth residuals

To identify which variables effectively capture the underlying post-drought trajectory of tree growth (RRW residuals), we tested two potential mixed-effects models that considered climate, stand structure, or stand age as predictors. CWD was chosen as the most appropriate climate variable related to drought conditions. Density of the plot was chosen as a proxy for intensity of competition, and stand age was used to examine the influence of forest age. For each of these three variables (CWD, total plot basal area measured in 2004, average stand age), the first model (Model A) included the explanatory variable as

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a fixed effect and a species random effect that allowed the intercept to vary by species. This accounts for each species having its own baseline growth. For the second model (Model B), we included the explanatory variable as a fixed effect, but we allowed both the slope and intercept to vary by species (residual ~ variable + variable|species). This allows the species to not only have different baseline growth rates, but different responses to the explanatory variables as well. Final model selection was based on the AIC, where the best fit model was the one with the smallest AIC (Appendix S1: Table S2). We then calculated the marginal and conditional R^2 for the regressions, reported p-values for Model B (Appendix S1: Table S3) and indicated which species' growth trajectories were significantly related to each variable ($p < 0.05$) for Model B (Figure 3A–C). In our models here, marginal R^2 quantifies the proportion of growth variance explained by fixed effects alone (CWD, basal area, and stand age), while the conditional R^2 includes both these fixed effects and the added explanatory power of species-specific differences (random effects).

Software packages

We implemented our analyses and plotting in R 4.2.1 via RStudio (R Core Team, 2022). The following R packages were used in our analyses and production of the figures: dplyr (Wickham et al., 2022), lme4 (Bates et al., 2015), tidyr (Wickham & Girlich, 2022), reshape (Wickham, 2007), data.table (Dowle & Srinivasan, 2021), Rvision (Garnier et al., 2021), MuMIn (Bartoń, 2024), ggplot2 (Wickham, 2016), gridExtra (Auguie, 2017), ggpubr (Kassambara, 2020), and plotrix (Lemon, 2006).

RESULTS

Statistical climate growth models and RRW residuals

Our process for selecting the best model for predicting RRWs during the baseline period (1960–1989) resulted in different models for each species. The model selected for aspen included precipitation, maximum temperature, soil moisture, PDSI, and SWE ($R^2{}_m = 0.07$, $R^2{}_c = 0.57$). The model selected for juniper included maximum temperature, soil moisture, and PDSI ($R^2{}_m = 0.079$, $R^2{}_c = 0.68$), and the same variables were selected for pinyon ($R^2{}_m = 0.06$, $R^2{}_c = 0.69$). The model selected for spruce included maximum temperature, precipitation, VPD, soil moisture, and PDSI ($R^2{}_m = 0.10$, $R^2{}_c = 0.59$). Finally, the model selected for ponderosa included SWE, AET, and PDSI ($R^2{}_m = 0.018$, $R^2{}_c = 0.78$). PDSI was included in the final models for all five of our species, indicating that it is consistently an important predictor of tree growth. Model fit statistics (e.g., $R^2{}_c$ and $R^2{}_m$) are summarized in Appendix S1: Table S1.

Applying the baseline models to post-drought (2002) years, for aspen, we observed positive growth signals for 3, 5, and 10 years post drought, as indicated by significantly positive RRW residuals ($p < 0.001$ for all three periods) (Figure 2A), indicating potential increases in available resources post drought (e.g., competitive release). For juniper, the RRW residuals were significantly greater than zero for 3 and 5 years post drought ($p < 0.01$), also an indication of competitive release; the residuals did not differ from zero 10 years post drought ($p = 0.96$) (Figure 2B). For pinyon, the RRW residuals were not significantly different from zero for 3, 5, or 10 years ($p = 0.65$, $p = 0.89$, and $p = 0.36$, respectively) post drought (Figure 2C). Both ponderosa and Engelmann spruce had residuals significantly less than zero ($p < 0.001$) for all three post-drought time periods (Figure 2D,E, respectively).

Comparing between binned years post-drought within a species using ANOVAs and post hoc Tukey tests, we found that there was no significant difference in RRW residuals between 3, 5, and 10 years post drought for pinyon ($p = 0.875$), and only a marginal difference for aspen ($p = 0.094$) and juniper ($p = 0.085$). In spruce, post-drought growth suppression decreased over 10 years, with the RRW residuals for 10 years being smaller than the 3 years ($p = 0.002$) and 5 years post-drought groups ($p = 0.003$), while 3 and 5 years post drought did not differ ($p = 0.99$). Ponderosa also showed a similar decrease in post-drought growth suppression through time, with 10-year residuals being smaller than the 3 years ($p = 0.009$) and 5 years post drought ($p = 0.002$), while 3 years and 5 years post drought did not differ ($p = 0.92$).

Mixed-effects models to explore unexplained variation in post-drought growth

For each of our three explanatory variables (CWD, average stand age, and total basal area in 2004), Model B, which allowed for both the intercept and covariate effects to vary by species, had a lower AIC than Model A, which only allowed for the intercept to vary by species. For the first explanatory variable (CWD), Model B yielded $R^2{}_c = 0.73$ and the regression of RRW residuals on CWD was significant ($p < 0.05$)

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for spruce, ponderosa, and aspen (Figure 3A). For total stand basal area, Model B gave $R^2_c = 0.78$, and the total stand basal area effect (coefficient) was significant ($p < 0.05$) for spruce, ponderosa, pinyon, and aspen, and was marginally significant for juniper ($p = 0.057$) (Figure 3B). The $R^2_c = 0.70$ for average stand age, which was significant ($p < 0.05$) for spruce and ponderosa (Figure 3D).

Dying species identity influenced legacies

We found that the identity of the species that died in each FIA plot partially mediated the post-drought changes in growth of surviving trees, particularly in pinyon-juniper woodlands (Figure 3D). Surviving juniper trees had higher growth than expected when mortality in the plot was dominated by a different species, generally pinyon. All aspen plots experienced mortality, and surviving aspen showed greater post-drought growth increases when the mortality in the plot was dominated by other conspecifics (aspen) compared to when aspen and a co-occurring species died. Surprisingly, ponderosa showed the largest reduction in growth compared to expected growth in plots for which no mortality was recorded in the FIA records. This may be because nearby mortality was not included in the radius of the FIA plots, or it could indicate the effect of competition such that in plots where all trees survived, those trees grew worse post drought compared to trees in plots where the canopy was thinned by mortality. Conversely, Engelmann spruce experienced the largest decrease in expected growth when spruce was the only species recorded to have died.

DISCUSSION

Species-specific growth responses to drought

We found that post-drought tree growth in forests in the southwestern United States is complex and species-specific, reflecting the broad ranging interactions among species traits, drought, and the competitive environment. Growth after a drought could either be lower than expected if the drought exerted long-lasting damage to the trees (Anderegg et al., 2013), or higher than expected if drought-induced mortality of neighbors freed up resources (e.g., water) for surviving trees (Chen et al., 2015; He et al., 2013), with the latter potentially reflecting the effect of competitive release (Chin et al., 2023). Post-drought growth in our study species, however, was typically of lower magnitude than what would be expected in the presence of competitive release suggested by timber harvest studies (Dore et al., 2012; Peña-Claros et al., 2008; Watson et al., 2020). These complex patterns may arise from variation in drought characteristics of each drought event (2002 and 2006), variation in drought tolerance across our species, and potential for long-term physiological impairment caused by drought.

We would expect drought-tolerant species to show higher post-drought growth and less mortality overall due to their ability to resist damage during drought. These species may support more intact xylem to take advantage of residual resources (water) following the drought event. As juniper is more drought tolerant than co-occurring pinyon (Linton et al., 1998) and showed greater relative post-drought growth than pinyon (Figure 2B,C), this could indicate a reduction in functional xylem in surviving pinyon trees that could not utilize increased water availability, whereas surviving junipers would likely be able to take advantage of such water sources. We did in fact observe these drought tolerance related patterns in mixed species plots in pinyon-juniper woodlands, although one previous study found that juniper did not directly benefit from the artificial removal of pinyon (Morillas et al., 2017). This interspecies variation highlights the importance of species-specific physiological traits in driving post-drought recovery. Surviving aspen also showed positive post-drought growth anomalies, perhaps due to an ability to produce new xylem relatively quickly, thus facilitating recovery from drought (Trugman et al., 2018). This high post-drought growth in aspen is consistent with modeling studies that showed recovery of growth following a drought may be important for recovering hydraulic capacity (Trugman et al., 2018) as the formation of new wood includes the creation of functional xylem (Rathgeber et al., 2016). Our results generally reflect a highly species-specific response to drought disturbance.

Mediators of post-drought growth

Despite the known importance of factors like climate and competition in influencing tree growth (Clark et al., 2010; McDowell et al., 2020), their specific roles in mediating post-drought growth responses remain a key area of uncertainty. Our study addresses this gap showing average stand age, CWD, and total live standing basal area were significant drivers of changes in growth after the severe 2002 drought, but their importance varied across species. Age was a significant mediator of post-drought growth in spruce and ponderosa plots. Although both species grew less than predicted after the 2002 drought given the post-drought climatic conditions, spruce plots had a positive correlation between residual RRW and stand age, while ponderosa was associated with a negative

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correlation between residual RRW and stand age. This is consistent with common ponderosa timber harvest approaches, which tend to be thinned earlier, when average stand age is approximately 10–15 years, before competition substantially decreases growth (DeGomez, 2006). Our study forests are significantly older than those generally managed for timber and therefore may have experienced the hypothesized reduction in intensity of competition that is often greater in older stands (Chin et al., 2023; Das et al., 2011; Keane et al., 2001; McCauley et al., 2022). Our findings, therefore, offer a unique perspective as they demonstrate how age-related competitive dynamics, particularly in unmanaged, older forests, can have a distinct and species-specific influence on an individual tree's capacity to recover from a major disturbance like drought. The differing relationships for spruce and ponderosa suggest that the role of competition in post-drought recovery is complex and not a uniform process across species, even within similar age classes.

Of our study species, spruce plots occurred in the wettest climates (highest elevation) and revealed a significant relationship between post-drought growth anomaly and CWD. Spruce plots that were wetter, with lower CWD, were associated with a greater reduction in post-drought growth relative to expected growth than spruce plots that were drier. This may reflect the common observation that high elevation forests are more often "energy-limited" (rather than water limited), and thus comparatively drier and lower elevation spruce sites had more available radiation and comparatively higher growth rates (Das et al., 2013). Ponderosa showed the opposite relationship: the drier a site, the greater the magnitude of growth reduction following the 2002 drought event. These findings suggest that the factors limiting post-drought growth are not uniform and depend on the climatic conditions of a site, which is critical for predicting forest resilience in a changing climate. Furthermore, this species-specific response highlights the need for a more nuanced understanding of how different species cope with drought-related stress. In addition, it is important to acknowledge that bark beetles are a large driver of mortality during and after drought in both ponderosa- and spruce-dominated forests (Hart et al., 2014; Negrón et al., 2009). Residual drought damage or pest infestations may have inhibited growth or caused additional mortality following the drought event. We attempted to control for this by selecting visibly healthy, mature trees for tree coring; however, there may have been a residual signal of past drought or insect damage.

For aspen and spruce, we found that trees in higher density forests grew significantly more than expected following the 2002 drought event, potentially indicating alleviation of higher pre-drought competition and highlighting the interaction between favorable climate conditions and potential for increased growth in relation to reduced competition (Ford et al., 2017). A recent review examining the effects of forest density reduction and drought-induced mortality in Mediterranean regions highlights the complex eco-hydrologic impacts of drought and vegetation removal (Tague et al., 2019). Changes in both groundwater recharge and streamflow can affect plant water availability in complex ways, resulting in differing outcomes based on forest eco-hydrology. Higher density aspen stands may also occur on the landscape in relatively wetter sites that are less impacted by droughts. These results suggest that for certain species and site conditions, drought-induced mortality could act as a natural thinning event, potentially enhancing the resilience of the surviving stand to future stress. Additional research in this area could complement tree ring measurements and shed further light on the mechanisms underlying competitive release and explicitly test how variations in site available soil moisture, soil texture, and subsurface and surface water flow affect post-drought tree growth.

Implications, limitations, and conclusion

Our analysis does not consider the duration, severity, and frequency of droughts, and our analysis explicitly removed plots where substantial mortality occurred during the second census interval and thus may disproportionately represent relatively healthier and wetter forests. Our analysis also assumes a stationary relationship between environmental predictors and tree growth, although recent studies have challenged this assumption (Wilmking et al., 2020) and have shown that increasing frequency of drought (and thus increasing frequency of drought legacies) is potentially a major source of non-stationarity (Peltier et al., 2022). Repeated drought events can exacerbate growth declines, particularly in ponderosa forests (Peltier & Ogle, 2019), and these legacy effects have been found to be especially extreme following more severe droughts (Anderegg et al., 2020). Therefore, it is difficult to separate the effects of competitive release, drought legacy effects on growth, and impacts of repeated drought, particularly given the temporally coarse nature of FIA surveys and therefore the ability to identify the timing of mortality.

Our results are associated with some caveats and limitations. Although the climatic variables were statistically significant in our growth models, the low R^2_m values indicate that these climate variables alone explain only a small fraction of the total variance in tree ring widths. This is a common feature of statistical analyses of tree rings, where factors such as site-specific conditions and tree-level characteristics contribute to growth but cannot be fully captured by climate variables alone. However, the relatively

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high R^2_c values, which increase substantially with the inclusion of plot as a random effect, indicate that the model's predictive power is primarily driven by spatial variability at the plot level. This suggests that plot-specific factors such as unmeasured local environmental conditions, microclimates, or other ecological variables play a substantial role in governing tree growth after a drought. The inclusion of plot as a random effect, therefore, significantly improves model fit and reflects the complex, multiscale nature of tree growth dynamics in response to climate.

In addition, it is important to acknowledge that the drought impacts may have been compounded by co-occurring beetle attacks in some tree species, particularly for the two pine species. This interaction complicates our ability to isolate the cause of mortality and attribute the subsequent changes in growth trajectories to drought alone. This is consistent with other studies identifying widespread drought mortality (Allen et al., 2010; Huang & Anderegg, 2012) and beetle attacks (Negrón et al., 2009) in the southwestern United States associated with the 2002 drought, a pattern supported by our in situ field observations made during tree core collection. A better understanding of pest and pathogen dynamics and defenses (Huang et al., 2020) and how they interact with tree physiology is an important frontier in understanding drought impacts on forests that could not be captured in the scope of this study (Trugman et al., 2021).

In conclusion, we show that the processes surrounding tree growth trajectories following drought are complex and highly species-specific. Developing a better understanding of complex eco-hydrologic processes and how they affect tree water resources during and after drought is an important future research avenue. Changes in water cycling processes, such as soil evaporation, run-off, groundwater recharge, canopy interception, and transpiration, can lead to feedbacks that put stands at further risk of death by drought (Goeking & Tarboton, 2020; Yaussy et al., 2013). Alternatively, positive growth anomalies of surviving trees—resulting from competitive release due to loss (mortality) of neighboring trees—may be able to offset impacts of future droughts and insect infestations on surviving trees (Edburg et al., 2012; Yaussy et al., 2013). This study sheds some light on the interspecific and intraspecific variation in response to drought across the southwestern United States, and our results help to inform further research focused on how large-scale biophysical processes and feedbacks are shaped by individual tree responses to drought.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Tree ring data (Zenes et al., 2025) are available from Figshare: https://doi.org/10.6084/m9.figshare.29901086.v1. R code used to conduct analyses and produce figures (Zenes, 2025) is available from Zenodo: https://doi.org/10.5281/zenodo.17566939.

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SUPPORTING INFORMATION

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

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