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RESEARCH ARTICLE

Trees in Fire-Maintained Forests Have Similar Growth Responses to Drought, but Greater Stomatal Conductance Than Trees in Fire-Excluded Forests

Kevin G. Willson[1] | Matthew D. Hurteau[1,2]

[1]Biology Department, University of New Mexico, Albuquerque, New Mexico, USA | [2]Center for Fire Resilient Ecosystems and Society, University of New Mexico, Albuquerque, New Mexico, USA

Correspondence: Kevin G. Willson (kevin.willson383@gmail.com)

ABSTRACT

In the western US, increased tree density in dry conifer forests from fire exclusion has caused tree growth declines, which is being compounded by hotter multi-year droughts. The reintroduction of frequent, low-severity wildfire reduces forest density by removing fire-intolerant trees, which can reduce competition for water and improve tree growth response to drought. We assessed how lower forest density following frequent, low-severity wildfire affected tree stomatal conductance and growth response to drought by coring and measuring competition surrounding ponderosa pines (*Pinus ponderosa*) in the Gila and Apache-Sitgreaves National Forests, New Mexico, US that either experienced 3–5 fires following long-term fire exclusion or remained fire-suppressed. We quantified tree growth declines during (resistance) and increases after (resilience) two recent multi-year droughts, which we compared between trees in fire-maintained and fire-excluded forests. We assessed stomatal conductance among trees by sampling wood from tree rings to measure stable carbon isotopes during and after both droughts, which we used to calculate evaporative water use efficiency. Trees in fire-maintained forests had greater resistance than trees in fire-excluded forests during the first drought, but growth responses became similar once the first drought ended. Interestingly, growth responses rarely varied despite evaporative water use efficiency increasing two times faster among trees in fire-excluded forests after the first drought commenced. Post-drought growth responses varied, in part, by aspect, with trees on northerly aspects exhibiting greater resilience to drought than trees on southerly aspects. Our results indicate that while trees had density-independent growth responses to drought, trees in fire-maintained forests were less water stressed than trees in fire-excluded forests. Therefore, the reintroduction of frequent, low-severity wildfire regimes has the potential to moderate some effects of hotter droughts as climate change intensifies.

1 | Introduction

Globally, tree die-off is increasing as a result of hotter droughts (Hammond et al. 2022). In semi-arid forests of the western US, hotter droughts are exacerbating the effects of increased competition that resulted from the exclusion of frequent-fire and the associated ingrowth of trees (Goulden and Bales 2019; Stephens et al. 2024; Williams et al. 2020). The reintroduction of frequent, low-severity wildfire can reduce forest density, which may lessen the impact of drought (Holden et al. 2007; Sohn et al. 2016; Zald et al. 2022). As semi-arid forests have become more flammable and prone to drought effects with increasing aridity (Abatzoglou

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et al. 2021, Gonzalez et al. 2018), determining how frequent wildfires affect tree response to drought is necessary to forecast forest function and response to future disturbances (van Mantgem et al. 2020).

Southwestern ponderosa pine (*Pinus ponderosa*) ecosystems historically had low forest density because of frequent, low-severity wildfires, which reduced the number of small, fire-intolerant trees on the landscape (Boucher and Moody 1998; Swetnam and Dieterich 1985). Starting around the turn of the 20th century, overgrazing and active fire suppression led to widespread fire exclusion, increasing the survival and recruitment of understory trees into the canopy that resulted in a 5–20-fold increase in forest density (Fulé et al. 1997; Moore et al. 1999, 2004). Greater forest density, coupled with hotter temperatures, has increased transpiration rates and reduced water availability for trees in southwestern forests (Andrews et al. 2020; Bréda et al. 2006). Lower water availability has increased competition for water, which governs growth in the region (Erickson and Waring 2014; Kerhoulas et al. 2013).

Competition for water increases during drought, which increases water stress among ponderosa pine and forces them to close stomata to reduce stomatal conductance and water loss (Strange et al. 2023; Lambers et al. 2008). Stomatal closure also reduces carbon uptake into the leaf, resulting in decreased growth during drought (Salmon et al. 2020; McDowell et al. 2003). Leaf-level gas exchange decreases more during drought among pines in more competitive growing environments (Zenes et al. 2020), reflecting larger increases in water stress (Simonin et al. 2007). Pines with greater competition and water stress also exhibit larger relative reductions in growth during drought (Sohn et al. 2016; Zald et al. 2022), indicative of lower resistance to drought (Lloret et al. 2011). Ponderosa pine growing in more competitive environments also remain water-stressed for longer periods after drought (Zenes et al. 2020), further limiting tree function like stomatal conductance and radial growth (Siegwolf et al. 2022). Reduced growth after drought is often a measure of a lower capacity for returning to pre-drought function, indicating that trees in competitive environments have, and flu lower resilience to drought effects (Lloret et al. 2011). Ponderosa pine in fire-excluded forests across the southwestern US has increasingly exhibited low resistance and resilience to recent droughts (Dannenberg et al. 2019), suggesting that increases in forest density and competition for water have increased tree water stress during and after periods of extreme aridity (Kannenberg et al. 2019).

The reintroduction of frequent, low-severity fire has the potential to reduce competition and tree water stress by reducing forest density (Holden et al. 2007; Sohn et al. 2016), which can improve tree growth responses to drought (Zald et al. 2022). Given the influence of frequent wildfire on forest density, we asked: Are trees growing in fire-maintained forests more drought-resistant and drought-resilient than trees in fire-excluded forests? We hypothesized that trees in fire-maintained forests would have smaller reductions in annual basal growth than trees in fire-excluded forests during drought because reduced competition would increase the amount of water available to trees. We also expected that

post-drought basal growth would return to pre-drought levels faster among trees in fire-maintained forests because transpiration rates would recover to pre-drought levels more rapidly than those of trees in fire-excluded forests.

2 | Methods

We tested our hypotheses by collecting data from fire-maintained and fire-excluded ponderosa pine forests to compare tree growth and stomatal responses to two recent multi-year droughts. We quantified tree growth and stomatal responses by collecting increment cores, from which we measured tree-ring widths to assess growth and carbon stable isotopes to assess stomatal conductance. We compared tree-ring widths and carbon stable isotopes using paired t-tests and explained variability in measured values using linear mixed models with a model selection framework, which provided causal explanations for similarities and differences in tree growth and stomatal responses during and after each drought.

2.1 | Study Sites

We collected data from ponderosa pine forests in the Gila and Apache-Sitgreaves National Forests, New Mexico, US (Figure 1). Ponderosa pine forests occur at mid elevations (1675–2590 m) in the region, with pinyon-juniper woodlands occurring at lower elevations and mixed-conifer forests occurring at higher elevations (Felger and Kindscher 2008). The climate of the region is semi-arid, with a mean annual temperature of 12°C and mean annual precipitation of 385 mm between 1990 and 2020 (https://www.ncdc.noaa.gov/cdo-web/datatools/normals, Gila Hot Springs station, New Mexico; 1706.9 m). The Gila experiences a bimodal precipitation regime, with snow in the winter and rain during the summer monsoonal period (Sheppard et al. 2002). Episodic drought is common and occurs at irregular intervals, ranging in frequency from once every several years to decades (Meko and Graybill 1995). Droughts also range in duration from a year to multiple decades (Pascolini-Campbell et al. 2015; Williams et al. 2022), with some events reaching magnitudes designated as extreme (Palmer Drought Severity Index < −4, Abatzoglou 2013). Soils in the region are a mixture of Ustalfs and Ustolls suborders (NRCS 2022).

Ponderosa pine forests in the region historically burned every 4–20 years at low severity, resulting in forests with densities that varied between 48 and 123 trees ha^{-1} (Garrett and Soulen 1999; Moore et al. 2004; Roccaforte et al. 2015; Ryan 2002; Swetnam and Dieterich 1985). Beginning in the early 1900s, widespread livestock grazing and fire suppression caused a cessation in wildfire, resulting in greater rates of ponderosa pine seedling survival that increased forest density (Covington and Moore 1994; Swetnam and Dieterich 1985). In 1924, the US Forest Service established the Gila Wilderness that prohibited most forms of forest and fuels management within wilderness boundaries, including forest harvesting, thinning, and prescribed burning. However, the establishment of a wildland fire use policy in 1975 gave managers the option of reintroducing wildfires in the Gila Wilderness (van Wagtendonk 2007). In the following 50 years, wildfires have burned throughout most of the Gila Wilderness,
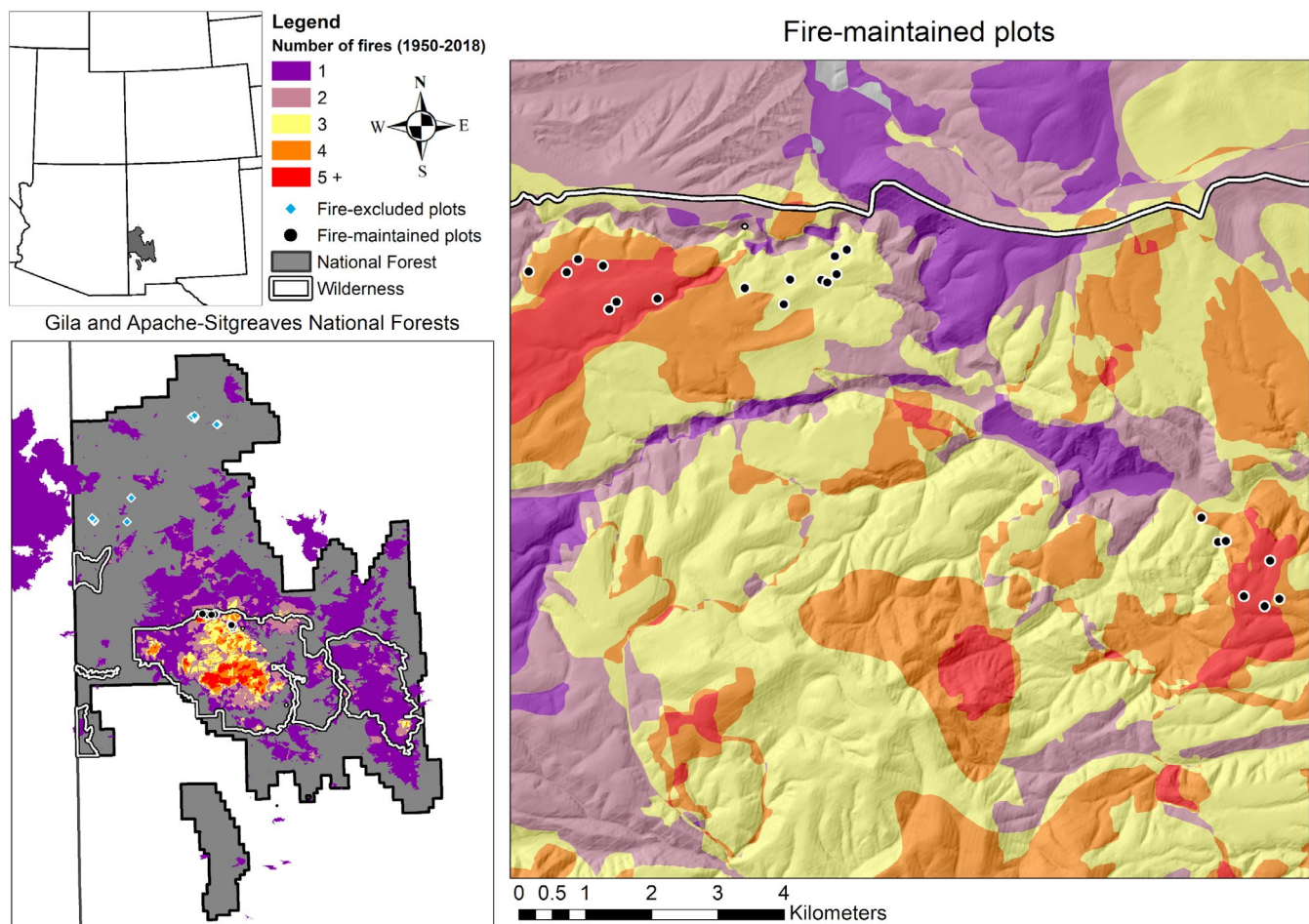
FIGURE 1 | Plot locations across the Gila Wilderness and Gila and Apache-Sitgreaves National Forests, New Mexico, US. Wilderness refers to undeveloped areas that are protected to preserve their natural state, including a ban on active forest management. The upper left panel shows the location of the Gila within New Mexico. The lower left panel shows the sampling locations of fire-maintained ($n = 22$) and fire-excluded plots ($n = 20$) and the number of fires that have burned locations in the region. The right panel shows the number of fires that have burned sampling locations in fire-maintained forests. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

with some locations experiencing surface fires at frequencies that are comparable to historical rates (Figure 1). However, forests outside of the Gila Wilderness have experienced few fires since the early 1900s, with many areas remaining fire-excluded.

2.2 | Data Collection

We established plots to measure stand structure and tree growth across ponderosa pine forests that had experienced no fire or multiple surface fires since the establishment of fire suppression policies. We used the LF 2016 version of the LANDFIRE dataset to identify potential sampling locations in ponderosa pine forests (Rollins 2009). We located areas that either had not experienced fire since 1909 or experienced multiple low-severity wildfires since 1950 using burn severity data from the Monitoring Trends in Burn Severity dataset (Eidenshink et al. 2007), corrected fire boundary data from Parks et al. (2015), and historical wildfire boundary records from Rollins et al. (2002). Within these areas, we sampled locations that experienced between three and five low-severity wildfires (hereafter fire-maintained forests) and places with similar elevation, slope, and aspect but no evidence of fire (hereafter fire-excluded forests; Figure 1).

To collect stand structure data, we established 22 plots in fire-maintained forests and 20 plots in fire-excluded forests, from which we identified candidate trees to collect growth, competition, and wood carbon isotope data. We quantified stand structure using a 0.2 ha circle plot to sample trees > 50 cm diameter at breast height (DBH), a nested 0.1 ha plot to sample trees between 15 and 50 cm DBH, and a nested 0.02 ha plot to sample trees between 5 and 14.9 cm DBH. Within each plot, we recorded DBH and species of all individuals, delineating all overstory ponderosa pine trees (DBH > 20 cm) as candidates for increment core sampling. We randomly selected 3–7 candidate overstory trees in each plot to collect increment cores. The number of sampled overstory trees varied by the number and size of candidate overstory trees in the plot with the purpose of capturing a representative distribution of overstory trees that was similar between fire-maintained and fire-excluded forests (supplemental Figure S1). We sampled two cores from each of 87 trees in fire-maintained forests and 83 trees in fire-excluded forests using a 5.15 mm increment borer. To collect wood for carbon isotopic analysis, we sampled an additional core from 92 of the cored trees using a 12 mm increment borer, including 46 trees each from fire-maintained and fire-excluded forests. We selected trees for isotopic analysis that accurately represented

overstory trees in each forest and resulted in comparable distributions of tree sizes between fire-maintained and fire-excluded forests. To quantify the competitive environment of cored trees, we measured all trees (> 5 cm DBH) within 5 m of all cored trees for DBH, species, and distance and direction from the cored tree (Frelich et al. 1998). Field data collection occurred between 2020 and 2022.

2.3 | Tree Core Processing and Analysis

We followed standard dendrochronological methods to dry, mount, and sand increment cores in preparation for growth measurements and carbon isotope analysis (Speer 2010). We scanned prepared cores using an Epson 12000XL scanner at 2400 dots per inch to date and measure tree rings. We measured annual tree-ring widths to 0.001 mm using WinDENDRO (Regent Instruments 2018). We statistically cross-dated cores between 1900 and 2018 using COFECHA (Holmes 1983). Once cross-dated, we averaged annual tree-ring widths between the two standard cores collected from each tree and detrended the resultant values using the modified negative exponential detrending method, which removes age-related growth trends (Cook and Kairiukstis 1990). This calculation provided tree-ring width index (RWI) values that represented standardized annual growth among trees.

After cross-dating isotopic cores, we sampled wood in growth rings from 1996 to 2018 to measure stable carbon isotopes before, during, and after two multi-year droughts. We used stable carbon isotopes to calculate evaporative water-use efficiency (eWUE; see methods below), which we used to assess tree stomatal conductance. We measured eWUE at annual timesteps during the years before, during, and after the two driest multi-year periods in the region since 1975, when wildland fire use policies were established in the Gila Wilderness (van Wagtendonk 2007). We delineated drought periods using the standardized precipitation evaporation index (SPEI), which represents a standardized measure of aridity to determine the onset, duration, and magnitude of drought (Vicente-Serrano et al. 2010). We calculated SPEI from 1975 to 2018 using monthly mean maximum temperature, monthly mean minimum temperature, and monthly precipitation totals with PRISM data that we converted to water years (October 1st through September 30th; PRISM climate group 2023). Using these values, we calculated potential evaporation-transpiration, climatic water balance, and SPEI using the spei package in R (Begueria et al. 2017, R Core Team 2023), which followed protocols from Vicente-Serrano et al. (2010).

To capture tree response to prolonged drought, we set the minimum drought length to 4 years, as antecedent effects from past climates can influence tree function for periods up to 4 years (Peltier et al. 2017). Using this minimum, we defined multi-year drought as periods with 4-year SPEI values below −1, a threshold often used to describe moderate-to-extreme drought (Slette et al. 2019). To account for drought periods greater than 4 years (Meko and Graybill 1995; Pascolini-Campbell et al. 2015; Williams et al. 2022), we included additional years to a drought when 4-year SPEI values remained below −1 for multiple, overlapping windows. Using this definition, we delineated 2000–2006 and 2011–2014 as the two drought periods (Figure S2).

To prepare samples for isotopic analysis, we manually excised approximately 1 mg of equal parts earlywood and latewood from each ring using a straightedge razor blade under a binocular microscope. We combined earlywood and latewood for isotopic analysis given the lack of evidence for seasonal fire effects on isotope values at resolutions our methods could reasonably capture (Battipaglia et al. 2014, Renninger et al. 2013, Ryan 2000, Sala et al. 2005, Tepley et al. 2020). Incorporating latewood into the isotopic analysis accounted for monsoonal-mediated influences on tree growth patterns, as latewood often relates to growth during monsoonal periods (Griffin et al. 2013). We avoided the first third of earlywood to minimize the influence of photosynthate from the previous growing season. We weighed and packed whole wood samples into tin capsules, which were analyzed using a Costech Elemental Analyzer connected to a Delta V Plus Mass Spectrometer via a Conflo IV Interface in the Center of Stable Isotopes located at the University of New Mexico. We used whole wood because past research indicated that whole wood and alpha cellulose samples provide similar environmental signals in their δ13C values (Weigt et al. 2015; Siegwolf et al. 2022).

2.4 | Data Analysis

To determine if growth response to drought varied between trees in fire-maintained and fire-excluded forests, we compared growth resistance and resilience among trees for each drought period. We assessed growth resistance using the relative reduction in growth that trees experienced during drought and growth resilience using the capacity of trees to return to growth rates comparable to pre-disturbance levels. We calculated resistance by dividing growth during drought by pre-drought growth and resilience by dividing post-drought growth by pre-drought growth, as outlined in Lloret et al. (2011). We quantified pre-drought growth for resistance calculations as the average RWI for the 7 years before the first drought and 4 years before the second drought. We quantified pre-drought growth for resilience calculations as the average RWI during the 4 years before drought. We quantified growth during drought as the average RWI during the 7 years of the first drought and 4 years of the second drought. We quantified post-drought growth as the average RWI during the 4 years after drought. We compared resistance and resilience scores between trees in fire-maintained and fire-excluded forests by calculating bootstrapped 95% confidence intervals using the smean.cl.boot() function from the Hmisc package in R (Harrell Jr 2023; R Core Team 2023).

To determine whether differences in competition influenced tree growth response to drought, we developed sets of linear mixed models to assess growth responses to each drought and used a model selection framework to select a final model from each set (Tables S1–S4). We modeled growth response to each drought using resistance and resilience as response variables, competitive environment, stand structure, climate, topography, and wildfire history as potential predictor variables, and plot ID as a random effect. We quantified the competitive environment using forest density, basal area, quadratic mean diameter, Heygi index, and growing space. We calculated the Heygi index using the following equation from Hegyi (1974):

$$Heygi\ index = \sum_{i=1}^{n} d_i / (d \times dist_i) \tag{1}$$

where d_i is the DBH of the ith neighbor tree, d is the DBH of the cored tree, and $dist_i$ is the horizontal distance from the ith neighbor tree to the cored tree within 5 m of the cored tree. We calculated the growing space of cored trees by creating Voronoi diagrams around each cored tree using the relative position of trees in the competitive environment and calculating the amount of area that was closest to the cored tree within each diagram (Aurenhammer 1991). This measurement assumed a similarly sized competitive environment surrounding cored trees that can vary from changes in biotic and abiotic features near each tree. Given inherent uncertainty about the size of competitive environments, we used a 5-m radius because of the high degree of neighborhood effects that are captured using a 5-m buffer (Frelich et al. 1998).

We quantified stand structure by calculating forest density, basal area, quadratic mean diameter, and accumulated aboveground biomass for each plot. We calculated accumulated aboveground biomass using allometric relationships of biomass and DBH by species with equations from Clary and Tiedemann (1986), Gower et al. (1992), Jenkins et al. (2003), and Kaye et al. (2005). We used stand structure variables to quantify long-term effects of frequent-fire on forests rather than fire severity after each fire because of recognized relationships between frequent-fire and stand structure, the effects of stand structure on tree stomatal conductance, and the multi-decadal scope of the study (Holden et al. 2007; Sohn et al. 2016). We quantified climate by calculating total precipitation, mean maximum temperature, mean maximum vapor pressure deficit, and mean SPEI at seasonal and annual timesteps by water year before, during, and after each drought using PRISM data. We also measured changes in climate by calculating differences in seasonal and annual climate variables between drought periods. We tested for and included additional periods when mean maximum temperature, total precipitation, and mean maximum vapor pressure deficit helped explain tree resistance and resilience, which we identified using the slidingwin() function from the climwin package (van de Pol et al. 2016).

We quantified topography using hillslope, elevation, northness, and topographic wetness index. We calculated northness by taking the cosine of aspect to quantify aspect as a continuous variable, with values of 1 representing due north, values of 0 representing due east or west, and values of −1 representing due south. We calculated aspect and hillslope in ArcMap 10.8 using 10 m digital elevation models from the USGS National Map(ESRI 2020, US Geological Survey 2020). We calculated topographic wetness index using the dyantopmodel package in R (Metcalfe et al. 2018). We quantified wildfire history by calculating the cumulative number of known wildfires that occurred in fire-maintained forests before, during, and after each drought and a binary value delineating if a tree experienced wildfire before, during, or after drought using methods outlined in Willson et al. (2024). We assigned all plot-level variables to each tree in the plot, including stand structure, wildfire history, topography, and climate data.

To select the final model for each response variable, we modeled all combinations of candidate predictor variables and assessed model performance for each. We selected candidate predictor variables by performing a correlation analysis to identify pairs of predictor variables with Pearson r correlation coefficients > 0.5,

retaining the predictor variable from each pair with a greater correlation value to the response variable (Dahlin et al. 2013). We assessed model performance among all combinations of candidate predictor variables by calculating the difference in AICc values (ΔAICc) among models using the dredge() function from the MuMln package (Bartoń 2023). We selected the final model from those with similarly high parsimony (ΔAICc < 2), either choosing the most parsimonious model or a model with additional predictor variables that were significant and measured at high resolution. We checked the normality of all model residuals using a Shapiro–Wilk test, multicollinearity using a variance inflation factor test, and homoscedasticity using a non-constant error variance test from the Car package in R (Fox and Weisberg 2019). We assessed all other assumptions graphically. To meet model assumptions, we performed a log or square root transformation on the response variable as necessary. We tested model fit by applying a leave-one-out cross-validation method to compare model performance and determine how model estimates were influenced by outliers using the Caret package (Hastie et al. 2009; Kuhn 2008).

To determine if stomatal conductance varied among trees in forests with different wildfire histories, we compared annual eWUE values between trees in fire-maintained and fire-excluded forests. To calculate eWUE, we converted $\delta^{13}C$ values to $\Delta^{13}C$ values following Farquhar et al. (1989), using $\delta^{13}C$ air records from Graven et al. (2017). Using $\Delta^{13}C$, we calculated the ratio of leaf internal to ambient $[CO_2]$ using equations outlined in Farquhar et al. (1989) and eWUE using the following equation from Strange et al. (2023):

$$eWUE = \frac{A}{E} = \frac{g_{CO_2(c_a-c_i)}}{g_{H_2O(e_i-e_a)}} = \frac{(c_a - c_i)}{1.6\ vpd} \qquad (2)$$

where A is carbon assimilation, E is the evapotranspiration rate, g_{CO_2} is the stomatal conductance of CO_2, g_{H_2O} is the stomatal conductance of H_2O, c_a is the atmospheric CO2 concentration, c_i is the intercellular concentration of carbon dioxide, e_i is the density of water vapor inside the leaf, e_a is the density of water vapor in the atmosphere, e_i–e_a is the local vapor pressure deficit (VPD) between the saturated leaf and unsaturated atmosphere, and 1.6 is the ratio of diffusivities of water vapor and CO_2. We used monthly VPD values from the PRISM dataset to calculate annual VPD for each water year and assumed that needle temperature was equal to air temperature to estimate leaf-level atmospheric moisture demand (Strange et al. 2023).

We compared annual eWUE values using paired t-tests and chronologies from each set of trees with 95% bootstrapped confidence intervals. We calculated chronologies of eWUE with 95% confidence intervals using the chron.ci() function from the dplR package (Bunn 2010). A comparison of eWUE chronologies between trees in fire-maintained and fire-excluded forests indicated that trees in fire-excluded forests had eWUE values that increased at greater rates during and after both droughts. To assess differences in the rate of change, we performed separate linear regressions for trees in fire-maintained and fire-excluded forests, using eWUE as the response variable and year as the predictor variable from 2000 to 2018.
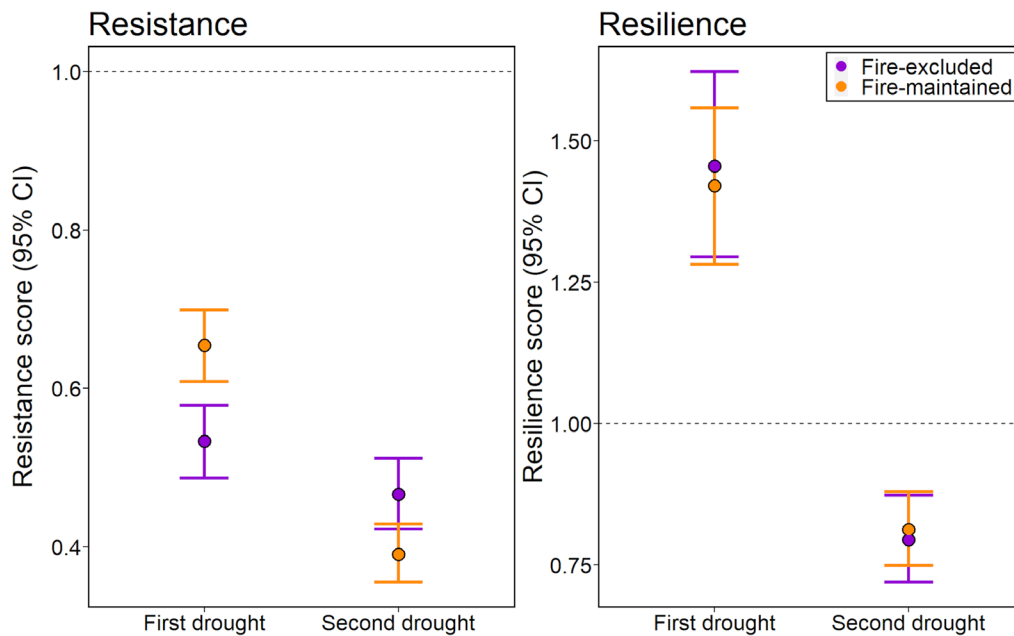
FIGURE 2 | Resistance and resilience scores with 95% confidence intervals (CI) among trees from fire-maintained (orange, $n_{trees} = 87$) and fire-excluded forests (purple, $n_{trees} = 83$). Resistance scores were calculated by dividing average RWI values during drought by average RWI values before drought. Resilience scores were calculated by dividing average RWI values after drought by average RWI values before drought.
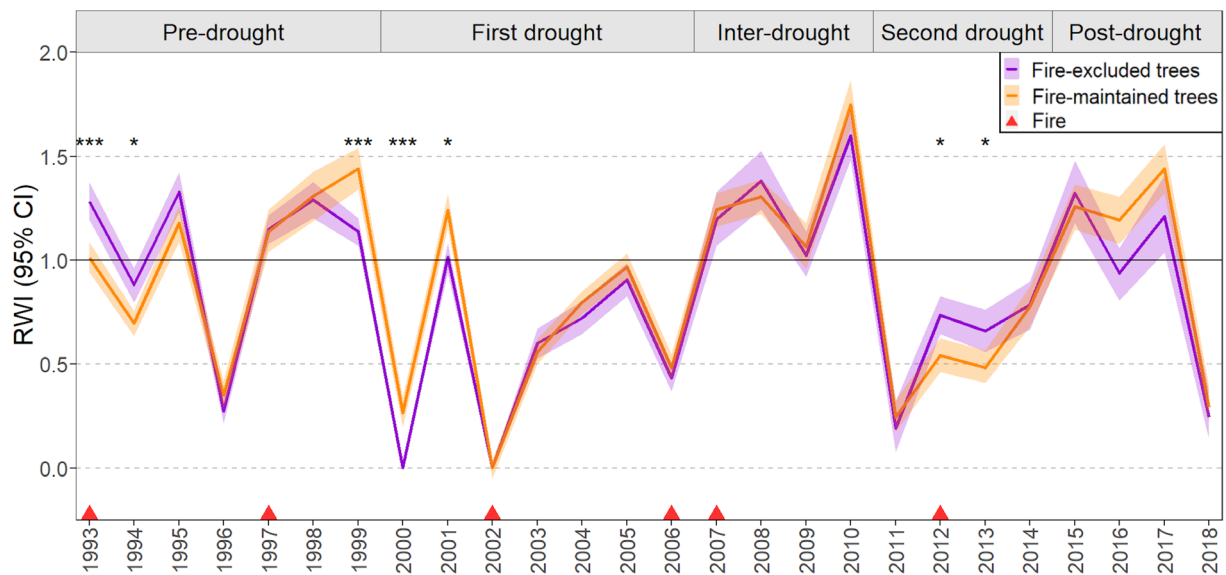

FIGURE 3 | Chronologies of annual tree-ring width index (RWI) values with 95% confidences intervals (CI) among trees from fire-maintained (orange, $n_{trees} = 87$) and fire-excluded forests (purple, $n_{trees} = 83$) delineated by drought period. The solid black line represents average growth (RWI = 1) across all trees from fire-maintained and fire-excluded forests. * represents $p < 0.05$, ** represents $p < 0.01$, and *** represents $p < 0.001$.

To determine how differences in competition and changes in climate influenced eWUE, we modeled annual eWUE values using a linear mixed model with a first-order autoregressive covariance structure. We modeled annual eWUE as the response variable, competitive environment, stand structure, climate, topography, and wildfire history as potential predictor variables, and plot ID as a random effect. We selected candidate predictor variables using a correlation analysis and used the dredge() function to identify the model with the most parsimonious fit. We checked the normality of model residuals using a Shapiro–Wilk test and graphically assessed all other statistical assumptions and isotopic relationships with tree size, tree age,

and growing space (Figures S3). The most parsimonious model included quadratic mean diameter at the stand scale. To determine if stand quadratic mean diameter differed between fire-maintained and fire-excluded forests, we performed t-tests by plots. All statistical analyses were performed in R version 4.3.2.

3 | Results

Trees in fire-maintained forests had 23% greater resistance to the first drought than trees in fire-excluded forests (Figure 2), with RWI values that were 0.23–0.26 units greater than trees
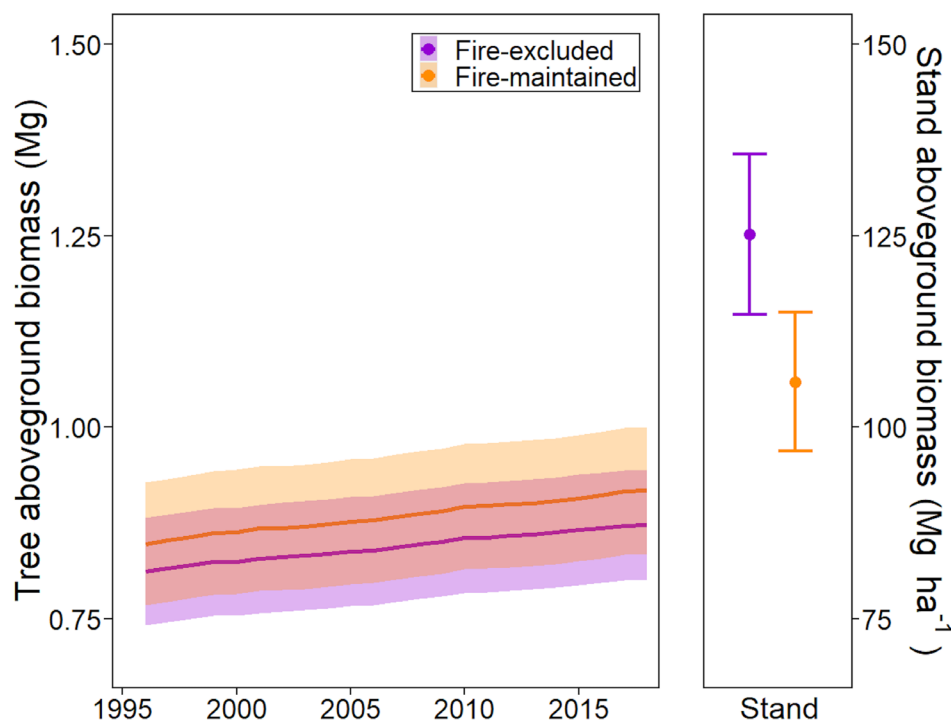
FIGURE 4 | Accumulated aboveground biomass (±one standard deviation) from fire-maintained (orange) and fire-excluded (purple) forests following fire reintroduction in fire-maintained forests. The left panel represents accumulated aboveground biomass of cored trees from fire-maintained ($n_{trees} = 87$) and fire-excluded ($n_{trees} = 83$) forests from 1996 to 2018. The right panel represents accumulated aboveground biomass of plots from fire-maintained ($n_{plots} = 22$) and fire-excluded ($n_{plots} = 20$) forests in 2020. Aboveground biomass was calculated using species-specific allometric relationships with measured tree diameter at breast height.

from fire-excluded forests during the first 2 years of the drought (Figure 3). However, there were few growth differences between trees in fire-maintained and fire-excluded forests after 2002, and both groups accumulated aboveground biomass at similar rates from 2002 to 2018 (Figure 4). As a result, trees from fire-maintained and fire-excluded forests had comparable growth responses after the first drought that varied with changes in aridity, differences in aspect, and shifts in precipitation (Table 1). Larger increases in springtime aridity caused greater reductions in resistance during drought, as tree resistance scores decreased by one for every three-unit decrease in spring SPEI during the first drought and by one for every three-unit increase in spring VPD during the second drought (Table 1). Stands on northerly aspects contained trees with greater resilience to the first drought than stands on southerly aspects, as resilience scores were 0.40 units greater among trees in north-facing stands (northness = 1) than trees in south-facing stands (northness = −1). Resilience increased with spring precipitation during the year after the second drought, as resilience scores rose by one for every additional 20 mm of precipitation that fell between March and May 2015.

We expected trees in fire-maintained forests to grow more during and after drought than trees in fire-excluded forests. However, this only occurred once among trees analyzed for isotopic discrimination after the first drought commenced (Figure 5). Interestingly, trees predominantly grew at similar rates despite using water at increasingly different efficiencies. Trees in fire-excluded forests used water more efficiently during all but 1 year, with eWUE values that were up to 15.5% greater than trees in fire-maintained forests. Trees

had similarly low water use efficiency values in 2000 (Fire-maintained eWUE = 5.53, Fire-excluded eWUE = 5.62), which represented the driest water year on record ($SPEI_{2000} = −2.38$) and coincided with the greatest difference in growth during the study period (Fire-maintained RWI = 0.33, Fire-excluded RWI = 0.00). After 2000, growth became similar while trees in fire-excluded forests became increasingly more water efficient, with eWUE values increasing two times faster during and after both droughts (Fire-excluded slope $_{eWUE} = 0.101$ mmol mol^{-1} year^{-1}, Fire-maintained slope $_{eWUE} = 0.047$ mmol mol^{-1} year^{-1}). Evaporative water use efficiency increased when trees received less precipitation during the prior water year and varied with aspect, as trees in south-facing stands assimilated 0.62 mmol more carbon per mol of water transpired than trees in north-facing stands (Table 2).

Fire-excluded forests, on average, had 541 trees ha^{-1} that were smaller than 30 cm DBH, which was over two times more than fire-maintained forests (234 tree < 30 cm DBH ha^{-1}, Figure 6). As a result, the quadratic mean diameter in the fire-excluded forest was 8.4 cm smaller and aboveground biomass was 18% greater than in the fire-maintained forest (Figures 4 and 6). Smaller average tree size helped explain differences in water use patterns between trees in fire-maintained and fire-excluded forests, as smaller stand quadratic mean diameter accounted for an estimated 15% increase in eWUE values among trees in fire-excluded forests (Table 2). Thus, trees in fire-maintained forests had growth responses to climate that were similar to trees in fire-excluded forests, but were much less efficient with water (Figure 5).

TABLE 1 | Fixed and random effects on estimates of growth resistance and resilience by drought. Random effects were represented by Plot ID ($n = 42$) in each model.

	Resistance				Resilience			
	First drought		Second drought		First drought		Second drought	
Predictors	Estimates	Std. Error	Estimates	Std. Error	Estimates	Std. Error	Estimates	Std. Error
(Intercept)	1.1083 ***	0.1142	1.6796 ***	0.2938	0.2556 ***	0.0444	−2.8522 ***	0.5599
Climate								
Change in spring SPEI	0.3903 **	0.1253						
Change in spring VPD			−0.3863 ***	0.0906				
Post-drought spring precipitation							0.0502 ***	0.0110
Topography								
Northness					0.1994 **	0.0667		
Random Effects								
σ^2	0.01		0.03		0.14		0.13	
τ_{00}	0.01 Plot		0.01 Plot		0.05 Plot		0.02 Plot	
ICC	0.28		0.22		0.26		0.15	
N	42 Plot		42 Plot		42 Plot		42 Plot	
Observations	171		168		170		170	
Marginal R^2/Conditional R^2	0.096/0.353		0.156/0.345		0.088/0.321		0.143/0.268	
RMSE	0.22		0.22		1.20		1.10	

**$p < 0.01$.
***$p < 0.001$.

4 | Discussion

Long-term fire exclusion has increased forest density and, with it, competition for water among trees in ponderosa pine forests. The fire-maintained forest we sampled had fewer small trees than the fire-excluded forest (Figure 6), which we expected would decrease competition for water, thereby increasing tree resistance and resilience to multi-year droughts. However, tree resistance and resilience rarely varied between fire-maintained and fire-excluded forests despite trees in fire-maintained forests maintaining greater stomatal conductance during and after two multi-year droughts (Figures 2 and 5). Instead, tree growth varied with climate and topography while stomatal conductance varied with climate, topography, and competition (Tables 1 and 2), resulting in a decoupled relationship between growth and stomatal responses to multi-year droughts.

Trees maintained greater stomatal conductance while growing in stands on northerly aspects and in stands with fewer trees (Table 2). North-facing stands retain more water than south-facing stands by receiving less solar radiation (Marsh et al. 2022), which reduces canopy air temperature, vapor pressure deficit, and leaf-level transpiration rates (Grossiord et al. 2020). Cooler, wetter conditions, when coupled with lower water use efficiency among trees, often signal greater water availability in forests

(Geroy et al. 2011). While we did not find an influence of aspect on growth resistance to drought, northness was an important predictor of resilience in both fire-maintained and fire-excluded forests (Table 1). Therefore, less incoming solar radiation may have resulted in greater water availability within north-facing stands once normal precipitation patterns returned, thus increasing resilience among residing trees.

The inverse relationship between stomatal conductance and forest density also aligned with expected tree responses to lower stand-level water use, less competition for water, and reduced water stress (Andrews et al. 2020; Bréda et al. 2006; Norlen et al. 2024). Furthermore, different stomatal responses indicate that ponderosa pine can alter its stomatal strategy in response to changes in fire regimes, suggesting an additional cause for variations in stomatal conductance among ponderosa pine populations during drought (Strange et al. 2023). However, fewer trees and greater stomatal conductance rarely coincided with greater growth among trees in fire-maintained forests (Figure 3), contradicting typical growth responses to density reductions in western US dry conifer ecosystems (Fulé et al. 2022; Hood et al. 2018; Sala et al. 2005). Trees normally grow faster following density reductions because of the inverse relationship between forest density and soil moisture, which often dictates growth in water-limited systems (Bréda et al. 2006, Boisramé
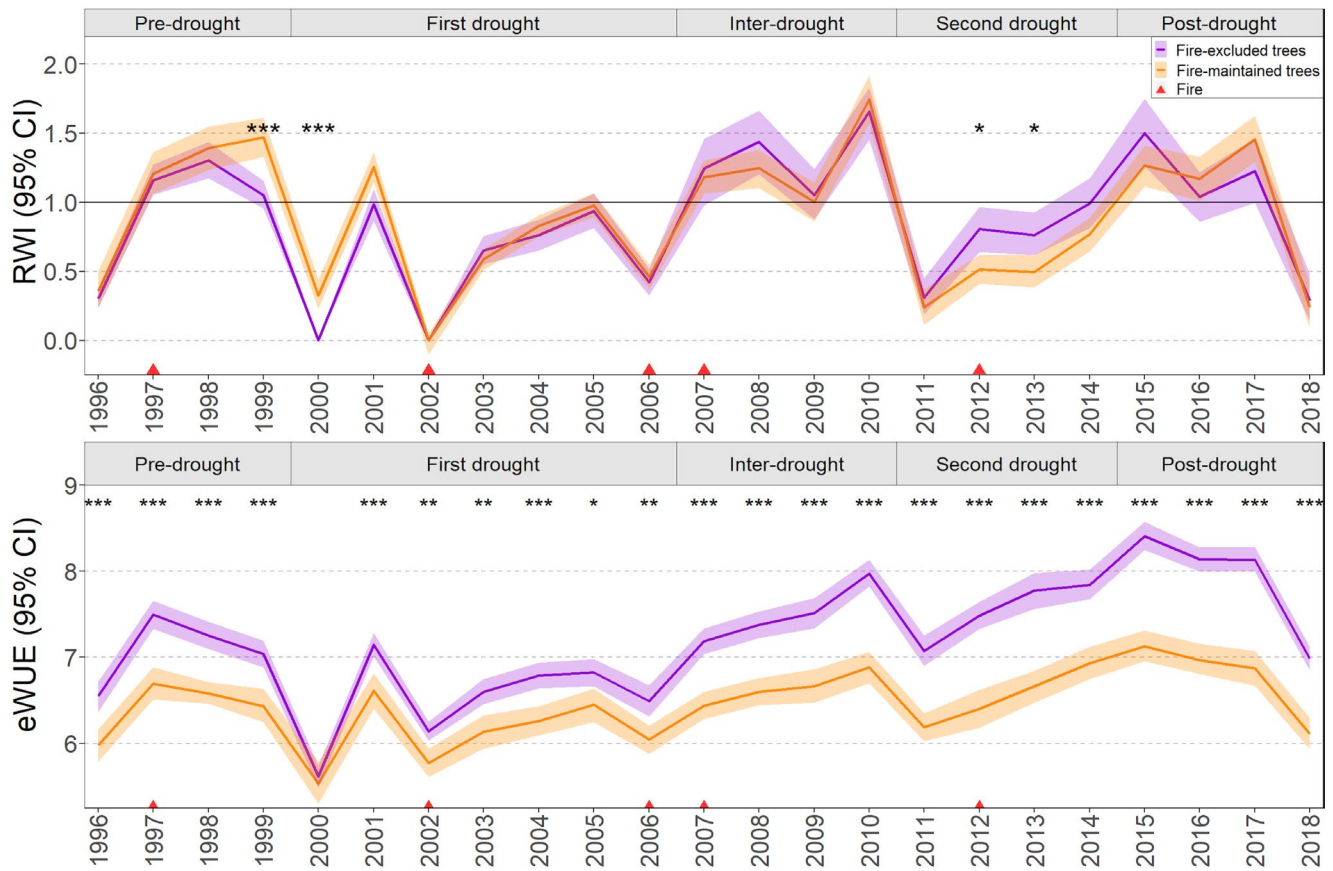
FIGURE 5 | Chronologies of tree-ring width index (RWI) and annual evaporative water use efficiency (eWUE) values with 95% confidences intervals (CI) among trees analyzed for isotopic discrimination from fire-maintained (orange, $n_{trees}=46$) and fire-excluded forests (purple, $n_{trees}=46$). The solid black line represents average growth (RWI = 1). Years are delineated by drought period. * represents $p < 0.05$, ** represents $p < 0.01$, *** represents $p < 0.001$.

et al. 2017). As a result, reductions in forest density frequently result in greater growth resistance and resilience to periods of aridity (Castagneri et al. 2022; Sohn et al. 2016; Zald et al. 2022).

Given tree growth response to density reductions in other studies, we were surprised by the apparent density-independent growth responses to climate among trees in both areas (Figure 3). Density-independent growth patterns may have resulted from trees employing conservative growth strategies in response to drought or growing at slower rates for several years after fire (Castagneri et al. 2022; Willson et al. 2024). Trees employ conservative growth strategies during drought to facilitate survival, investing resources into metabolic pathways unrelated to growth, such as defense, respiration, and osmoregulation, which can cause trees to have similar growth patterns while photosynthesizing at different rates (Ferrenberg et al. 2023; Hartmann and Trumbore 2016). Trees often use these strategies in response to periods of extreme aridity (Carnwath and Nelson 2016, Dannenberg et al. 2019), which may explain similar growth patterns during and after increasingly hot droughts (Williams et al. 2022).

Similar growth patterns may have also resulted from post-fire growth reductions among burned trees. Fire reduces growth by damaging the leaves, roots, xylem, and cambium of trees (Hood et al. 2008; Michaletz et al. 2012; Wagner 1973), which lowers their photosynthetic capacity and growth rate compared to unburned trees (González-Rosales and Rodríguez-Trejo 2004, Hood

TABLE 2 | Fixed and random effects on estimates of annual evaporative water use efficiency (eWUE). Random effects were represented by Plot ID ($n = 42$) in each model.

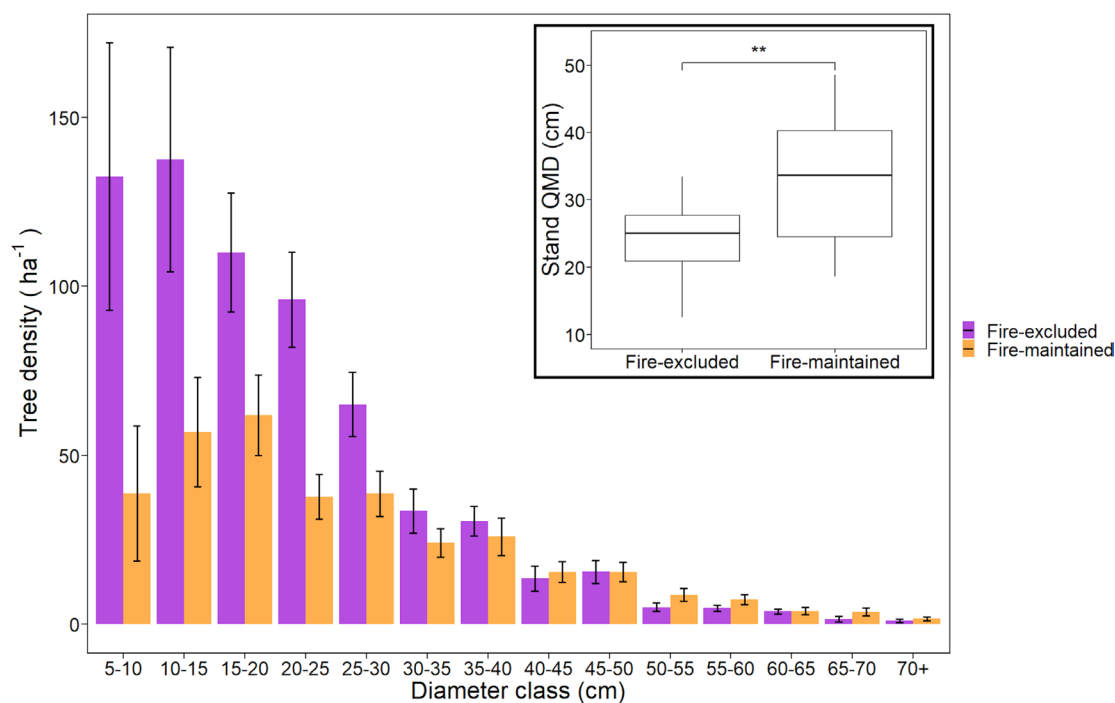| Predictors	Annual eWUE	
	Estimates	**Std. error**
(Intercept)	8.9123***	0.3140
Fixed effects		
Prior water year total precipitation	−0.0021***	0.0001
Northness	−0.3011*	0.1295
Stand quadratic mean diameter	−0.0411***	0.0101
Random effects		
σ^2	0.47	
$\tau_{00\ Plot}$	0.21	
ICC	0.31	
N_{Plot}	36	
Observations	2114	
Marginal R^2/Conditional R^2	0.179/0.434	
RMSE	0.68	

*$p < 0.05$.
***$p < 0.001$.

FIGURE 6 | Tree densities (±one standard error) by diameter class in fire-maintained (orange, $n = 22$ plots) and fire-excluded (purple, $n = 20$ plots) forests. The inset shows boxplots of quadratic mean diameter (QMD) in fire-maintained and fire-excluded plots. ** represents $p < 0.01$.

et al. 2018, O'Brien et al. 2010). Interestingly, growth among our frequently burned trees broadly remained similar to the growth of unburned, fire-excluded trees during and after both droughts. The similarities in growth may imply that short-term growth reductions after wildfire obscured the effects of reduced competition and water stress on growth following decades of frequent fire. If so, our findings suggest that improved growing conditions caused by frequent fire can help trees resist drought more effectively than those in fire-excluded environments, except during periods immediately following wildfire. As wildfires and drought are projected to become more frequent with additional climate warming (Abatzoglou et al. 2021, Gonzalez et al. 2018), it would be beneficial for future research to dissect the interactive effects of wildfire and drought on tree vigor and forest function by increasing the sample of trees to capture extended periods when drought and wildfire did not co-occur.

We made several assumptions about forest stand dynamics, photosynthetic assimilation, metabolic pathways, and leaf-level water loss during the course of our study. First, we used a single measurement of stand structure and the competitive environment as a proxy for past growing conditions that may have varied over the prior 26 years. While relative differences among sites likely remained reasonably consistent, our analytical approach did not account for decadal changes in stand structure and competition caused by frequent fire that can alter tree water use and growth (Chamberlain et al. 2023; Sohn et al. 2016). Additionally, we calculated water use efficiency using stable carbon isotopes, which assumes constant rates of stomatal conductance despite trees growing in different microclimates (Grossiord et al. 2020; Marsh et al. 2022). Furthermore, we assumed that trees invested a comparable proportion of resources into growth during drought (Hartmann and Trumbore 2016). These assumptions may have limited our ability to mechanistically explain the

decoupled growth and isotopic response to drought among trees in fire-maintained forests. Overcoming the need to make these assumptions would require more frequent measures of stand dynamics, measures of resource investment into defense, respiration, and osmoregulation, and increased spatial resolution of water use patterns. Given our results, collecting transpiration data via sap flow measurements, defense data via annual resin duct production, respiration data via leaf-level gas exchange, and osmoregulation data via leaf-level pressure volume curves may provide additional insight into this response.

Trees have become increasingly susceptible to mortality during and after droughts because hotter temperatures have reduced tree access to water and increased tree vulnerability to compound disturbances (Allen et al. 2015; Choat et al. 2018). Our findings demonstrate that the reintroduction of frequent, low-severity wildfire moderates some effects of hotter drought, as lower forest density alleviated tree water stress without impacting growth responses to multi-year droughts (Figure 5). Less water stress often signals smaller declines in tree function and less vulnerability to drought-induced disturbances (Bernal et al. 2023; Férriz et al. 2021; Linares and Camarero 2012; McCullough and Wagner 1987), which corroborates findings that trees in fire-maintained forests are less susceptible to drought-induced mortality than in fire-excluded forests (Norlen et al. 2024). As droughts are anticipated to become hotter and longer (Yuan et al. 2023), the reintroduction of frequent, low-severity wildfire may mitigate some detrimental effects of drought and reduce the risk of tree die-back in semi-arid forests.

Author Contributions

Kevin G. Willson: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, validation,

visualization, writing – original draft, writing – review and editing. **Matthew D. Hurteau:** conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, re-sources, supervision, validation, writing – review and editing.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available in Dryad at http://doi.org/10.5061/dryad.d7wm37q9w. PRISM climate data were obtained from the Oregon State PRISM Group da-tabase, accessible at https://prism.oregonstate.edu/. LANDFIRE LF16 data were obtained from the LANDFIRE working group database at https://landfire.gov/. Fire severity data were accessed from the Monitoring Trends in Burn Severity program from the U.S. Geological Survey data release at https://doi.org/10.5066/P9IED7RZ. Digital eleva-tion models were accessed from the US Geological Survey National Map at https://data.usgs.gov/datacatalog/data/USGS:3a81321b-c153-416f-98b7-cc8e5f0e17c3#:~:text=1/3rd%20arc%2Dsecond%20Digital%20Ele vation%20Models%20(DEMs)%20%2D,is%201/3%20arc%2Dsecond%20 (approximately%2010%20m)%20resolution.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.