Sixty-five years of fire manipulation reveals climate and fire interact to determine growth rates of *Quercus* spp.

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**Abstract.** Minimizing forest vulnerability to more frequent and severe droughts, as climate models predict, has emerged as a primary goal of forest management. One potential strategy to moderate drought-induced stress is reducing basal area through the repeat application of prescribed fire. However, use of prescribed fire as a management tool to reduce drought vulnerability has been largely untested. Here, we report the long-term effects of repeat fires on the climate-growth response of adult oaks (*Quercus* spp.) in the Missouri Ozarks, USA. We measured the annual radial growth of trees that experienced either no fire, periodic (every 4 yr), or annual prescribed fires from 1950 to 2015. To assess whether increased fire frequency interacts with climate to determine long-term forest productivity, we modeled annual growth as a function of potential evapotranspiration, fire treatment, and their interaction. We also quantified the effect of fire-driven reductions in tree density on carbon and oxygen isotope composition of tree rings and drought resistance (growth during drought) and resilience (growth recovery after drought) during past drought events. Annual radial growth and isotopic composition data indicated trees experienced reduced growth due to moisture stress, but drought vulnerability did not vary between frequently burned forests and unburned controls. In contrast, periodic, but not annual, fires reduced annual growth by 9.6% during wet periods favorable to growth with the effect consistent over time. Fire had minimal effects on total and inorganic soil nitrogen after 65 yr of treatment, regardless of frequency, suggesting other underlying causes of the observed growth declines under periodic burning (e.g., crown, bole, or root injury). Our results suggest that long-term, increased fire frequency can have negative effects on long-term tree growth, but effects are contingent upon the fire return interval. These findings highlight important differences in how fire and thinning influence density-dependent competition and the response of tree growth to climate. Although additional studies are needed from other forest ecosystems, this study provides early evidence that increased fire frequency will not alleviate drought stress and instead, may reduce long-term, aboveground carbon storage in forests.

**Key words:** climate change adaptation; drought; fire; nitrogen availability; oak-hickory; radial growth; resilience; resistance; stand density; temperate broadleaf forest; water stress.

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INTRODUCTION

Projected changes in temperature and rainfall patterns with climate change are expected to increase drought stress in forests, with widespread, negative consequences for forest productivity (Choat et al. 2012, Anderegg et al. 2015). Drought-induced reductions in tree growth may threaten carbon (C) sequestration rates, including highly productive, temperate deciduous forests of eastern North America (Pan et al. 2011, D’Orangeville et al. 2018). Developing management strategies to increase adaptive capacity may help mitigate or reduce forest vulnerability to this change (Millar et al. 2007), and several recent studies suggest that forest thinning can be one such promising approach (D’Amato et al. 2013, Sohn et al. 2016b, Bradford and Bell 2017, Bottero et al. 2017). By reducing forest basal area, thinning effectively increases water availability to the remaining trees, thereby reducing forest vulnerability to drought.

Despite its widespread use, prescribed fire has been largely overlooked as a management tool to minimize ecosystem vulnerability to climate change (but see van Mantgem et al. 2016). Increased fire frequency may influence the drought response and recovery of trees through its effects on forest structure, species composition, and soil nutrient availability. Frequent fires reduce stem density (Peterson and Reich 2001) and kill fire-intolerant tree species (Knapp et al. 2015), which in turn can reduce transpiration and competition for water and increase subsurface water availability (DeBano et al. 1998). However, frequent fires may also compound drought-driven reductions in forest productivity through its effects on soil nitrogen (N) availability. Over decades, repeat surface fires can reduce soil N availability through volatilization (Raison 1979), reduced forest floor organic matter, and declines in mineralization rates associated with greater grass abundance (Wedin and Tilman 1990, Reich et al. 2001), with the magnitude of these effects dependent on fire return interval and intensity (DeBano et al. 1998). Fire-driven declines in soil N availability may strongly constrain the recovery of tree growth after drought and continue to limit forest productivity under more favorable moisture conditions, especially with frequent fire (Reich et al. 2001, Carter and Darwin Foster 2004, Pellegrini et al. 2018). Depending on whether fire-driven reductions in density-dependent competition (sensu McDowell et al. 2006, Bottero et al. 2017) or N availability predominate, changes in prescribed fire frequency may have positive, negative, or neutral consequences for the drought vulnerability of trees and, consequently, forest productivity under climate change (Biondi 1999). Examining the long-term effects of repeat prescribed fires on forest productivity in relation to climate variability and, in particular, drought events, is necessary to determine whether fire is an effective tool for increasing the adaptive capacity of forests.

The effects of fire on forest vulnerability to climate change may not be immediately apparent because of the lagged response and recovery of tree growth from fire disturbance and climate-related stress (Bréda et al. 2006). Tree-ring records are thus critical for detecting growth responses and understanding cumulative impacts from recurring fire (Reich et al. 2001). Although rare, long-term experiments that have manipulated prescribed fire frequency for decades provide an unparalleled opportunity to understand the immediate and lagged effects of fire on forest drought vulnerability. When used in tandem, radial growth and the carbon (\(\delta^{13}\text{C}_{\text{R}}\)) and oxygen isotopic composition (\(\delta^{18}\text{O}_{\text{R}}\)) of annual radial growth rings provide complementary, historical records of tree growth and drought stress, respectively. In C\(_3\) plants, \(\delta^{13}\text{C}_{\text{R}}\) provides a long-term record of leaf-level intrinsic water use efficiency (WUE\(_i\)), given by the ratio between net photosynthesis rate and stomatal conductance (Farquhar et al. 1989), while \(\delta^{18}\text{O}_{\text{R}}\) provides a time-integrated indication of leaf stomatal conductance during the growing season, thereby helping to disentangle the independent effects of photosynthesis and stomatal conductance on WUE\(_i\) (Barbour 2007). Plants typically minimize water loss during drought through stomatal limitation of photosynthesis. Therefore, low radial growth accompanied by high WUE\(_i\) and \(\delta^{18}\text{O}_{\text{R}}\) (i.e., more enriched) values indicate severe past drought stress, whereas low radial growth without higher isotopic values indicates a factor other than moisture was limiting.

To assess the long-term, interactive effects of fire and climate on forest productivity, we leveraged a unique, long-term fire manipulation experiment in the Missouri Ozark Plateau, USA, to
compare annual radial growth patterns and the stable isotope composition of tree rings from adult oak (*Quercus* spp.) trees experimentally exposed to differing fire frequencies for the past 65 yr. We paired these growth data with data on stand density and soil N availability across treatments to explicitly test the density-dependent effects of fire on climate-growth patterns while also considering the potential for fire-driven effects on N cycling to influence tree growth. We tested the following two hypotheses: (H1) If increased fire frequency reduces density-dependent competition for water, then burned stands will show reduced population-level water stress signals (i.e., lower WUEi and depleted δ18O_R signatures) and greater resistance and resilience in annual growth to past drought stress than unburned stands; and (H2) If increased fire frequency intensifies nitrogen limitation, then individuals in burned stands will have reduced annual growth rates relative to unburned individuals, especially during wet periods favorable for growth. Further, if effects are cumulative, then the cumulative growth of burned and unburned trees should diverge over time. Considering continued climate change in the future, our work sheds light on how fire treatments on stand structure are fully described elsewhere (Knapp et al. 2015, 2017a); we summarize the most relevant findings here. In 2013, after 63 yr of treatment, annual and periodic burns had reduced mean stand basal area by 16% and 26%, respectively, and adult tree density by 25% and 44%, respectively, relative to controls (Table 1; Appendix S2: Plate 2, Fig. S1). Canopy leaf area index (LAI) in 2013 was reduced by 33% and 47% in annual and periodic burned treatments, with average flame lengths ranging from 1–3 and 1–5 feet for annual and periodic burned plots, respectively (Appendix S2: Plate 1). In general, bole char was uncommon after treatment, and no evidence of direct crown injury has been observed. Each block includes two replicate plots of each treatment, for a total of four plots per treatment. A single fire was used to burn the replicate annual and periodic plots within one of the blocks; therefore, replicate plots were not considered independent for the purposes of analysis. For more details on the experimental design, see Knapp et al. (2015).

The effects of the fire treatments on stand structure, mean tree diameter in 2013 was greater for populations in annual and periodic burned treatments than controls, predominately due to the lack of small stems (dbh ≤ 20 cm) in burned plots (Table 1; Appendix S2: Fig. S2).

**Meteorological data**

Daily climate variables were obtained from the National Oceanic and Atmospheric Administration (NOAA): daily mean temperature, maximum temperature, minimum temperature and precipitation. Climate data cover the period 1948–2015 and were collected from the Wappapello (Butler County, Missouri) and Greenville...
Wayne County, Missouri) stations located within 20 km of the study site. Additionally, we obtained daily wind speed and dew point data from Poplar Bluff, Glennonville and Rolla, Missouri stations, and global solar radiation data from the National Solar Radiation Database (NSRDB).

We used daily climate data to calculate eight climate variables, including potential evapotranspiration (PET), averaged over a 7-month and 19-month time period for each year (see Appendix S1). The 7-month period comprised April–October of the year of ring formation, whereas the 19-month period comprised April of the year prior to ring formation through October of the year of ring formation. The 19-month period allows inclusion of the previous year’s growing season, intervening winter/spring and growing season during the year of ring formation. This is a standard approach in tree-ring analysis, as it allows evaluation of effects of preconditioning by climate before the growing season (Cook and Kairiukstis 1990). Furthermore, the growth of upland oak species is often highly correlated with the previous year’s climate (White et al. 2011).

**Selection of target dry and wet years**

To identify growing seasons with limiting and non-limiting soil water availability during the study period, we estimated the daily relative extractable water in the soil (REW, unitless). REW is the ratio of available soil water to maximum extractable water (i.e., water holding capacity) and varies between 0.0 (permanent wilting point) and 1.0 (field capacity). An REW of >0.4 indicates soil water conditions are non-limiting for transpiration for a large range of tree species, whereas an REW of <0.4 indicates a soil water shortage severe enough to reduce stomatal conductance and radial growth (Granier et al. 1999). We used the BILJOU forest water balance model to calculate daily REW for the study site for the duration of the experiment (1951–2015; Granier et al. 1999; Appendix S1).

To determine annual water stress, we calculated an index (unitless; Granier et al. 1999, Grossoird et al. 2014) that summarizes the number of days soil water was limiting for growth:

\[
\text{Waterstress index} = \frac{1}{0.4} \times \sum_{j} (0.4 - \text{REW}_j)
\]  

(1)

where \(j\) corresponds to the days when REW is < 0.4. Using this index, we selected one to two target dry years with the greatest water stress index for each decade, with the exception of the generally wet decades of the 1970s and 1990s, from which no years were selected (Fig. 1a; Appendix S1: Table S1). The dry years of 1953

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**Table 1. Summary of stand structure in unburned control, annual, and periodic (every four years) burn treatments.**

| Characteristic            | Control          | Annual          | Periodic         |
|---------------------------|------------------|-----------------|------------------|
|                           | Mean  | SE   | Mean  | SE   | Mean  | SE   |
| Basal area (m²/ha)        |       |      |       |      |       |      |
| Carya spp.                | 4.33  | 0.01 | 1.33  | 0.01 | 2.17  | 0.02 |
| Cornus florida            | 0.01  | ...† | ...‡  | ...  | ...   | ...
| Other                     | 0.18  | 0.04 | 0.03  | ...  | ...   | ...
| Quercus alba              | 1.37  | 0.02 | 0.71  | 0.01 | 1.01  | 0.04 |
| Quercus coccinea          | 0.31  | 0.02 | ...   | ...  | 0.52  | 0.03 |
| Quercus falcata           | 3.76  | 0.02 | 2.77  | 0.01 | 1.48  | 0.01 |
| Quercus stellata          | 9.59  | 0.01 | 11.63 | 0.00 | 9.79  | 0.00 |
| Quercus velutina          | 3.31  | 0.01 | 2.81  | 0.02 | 2.07  | 0.01 |
| Ulmus alata               | 0.02  | ...  | 0.03  | ...  | ...   | ...
| Total                     | 23.06 | 1.64 | 19.29 | 0.95 | 17.04 | 0.83 |
| Density (stems/ha)        |       |      |       |      |       |      |
|                           | 332.81| 15.81| 250.00| 18.40| 185.94| 31.70|
| dbh (cm)                  | 24.35 | 0.91 | 26.96 | 1.23 | 29.60 | 1.06 |
| LAI                       | 3.01  | 0.35 | 2.05  | 0.19 | 1.63  | 0.21 |

**Notes:** Data on basal area (BA, m²/ha), stem density, and diameter at breast height (dbh) were collected in 2013 from adult trees (≥10 cm dbh). Canopy leaf area index (LAI) was collected in 2010. Data from Knapp et al. (2015).

† Species present in a single plot.

‡ Species not present.
and 1954 were considered one multi-year drought event. For each decade we selected a dry year, we selected an accompanying wet year with a water stress index < 6.0 (arbitrary threshold; Grossiord et al. 2014; Fig. 1a; Appendix S1: Table S1).

**Dendroecological analysis**

We collected increment cores in March 2015 from 173 trees (≥10 cm dbh) from the two most abundant oak species: *Q. stellata* and *Q. falcata*. We were interested in the stand-level response to fire treatments, and therefore, we randomly selected individuals inside each plot (n = 12) to obtain a sample size for each species that was proportional to their abundance in the field (Knapp et al. 2015). Although *Q. stellata* was most abundant, both species were well-represented across all treatments (Appendix S2: Table S1). For each tree, we used a Hagløf borer to extract one 5 mm diameter core from the southern side of the trunk at breast height. Cores were stored in paper straws and allowed to air-dry. In the laboratory, cores were sanded until

![Fig. 1. (a) Annual potential evapotranspiration (PET) for the study site during the period 1948–2015. Targeted dry and wet years are indicated as vertical dashed and dotted lines, respectively (see Methods). Mean (± SE) annual basal area increment (BAI) per tree for (b) *Quercus falcata* and (c) *Quercus stellata* in unburned control, annual, and periodic burn plots during the duration of the experiment (1950–2015). Means are calculated from all measured individuals per treatment.](image-url)
tree rings were clearly visible. Visual cross-dating of cores was done separately for each species, block, and fire treatment and dates checked using COFECHA software (Holmes 1983). The characteristics of the final chronologies are summarized in Appendix S2: Table S1. After correcting for any dating errors, annual ring-width measurements were made to 0.01-mm precision using the Velmex TA measurement system and MeasureJ2X software (VoorTech Consulting, Holderness, New Hampshire). To model tree growth, we converted annual ring-widths (cm/yr) to basal area increment (BAI, cm²/yr) using the dplR package in R (Bunn 2008).

**Growth ring δ¹³C and δ¹⁸O**

We extracted latewood sections for each target dry and wet year using a razor blade, grouped the sections by year and species, and pooled the samples into two to three subsamples per plot (referred to as “pools” hereafter; Appendix S2: Table S2) to improve homogeneity and increase the amount of material for analysis. We homogenized each pooled sample using 6-mm solid borosilicate beads and a bead mixer. We selected only latewood because the δ¹³C signature of latewood mainly characterizes the functioning of trees during the second part of the growing season and avoids potential effects related to a favorable spring climate or the remobilization of stored photosynthates from the previous growing season (Offermann et al. 2011). We did not perform alpha-cellulose extraction of the bulk sample because cellulose and bulk wholewood have been found to yield highly correlated signals (Loader et al. 2003). Homogenized samples were weighed using a high-precision balance (±0.001 mg), and separate subsamples were placed into tin and silver capsules for carbon and oxygen isotope analyses, respectively. The carbon and oxygen isotopic analyses were done on a Thermo Fisher Delta V Advantage isotope ratio mass spectrometer (Fisher Scientific, Waltham, Massachusetts, USA) at the University of Illinois. For oxygen isotopic analysis, samples were pyrolyzed to carbon monoxide at 1450°C in a high-temperature elemental analyzer (Thermo Fisher TC/EA). The precision of the analyses was better than 0.1‰ for δ¹³C and 0.2‰ for δ¹⁸O. Isotope ratios are expressed in delta notation (‰) relative to the reference standard: V-PDB for δ¹³C and V-SMOW for δ¹⁸O.

We calculated annual intrinsic water use efficiency values (WUEi) from the carbon isotopic composition of individual radial growth rings (δ¹³C_R) using the model described by Farquhar et al. (1982):

\[
WUE_i = \frac{c_a (b - \Delta \delta^{13}C)}{1.6(b - a)}
\]

with

\[
\Delta \delta^{13}C = \frac{\delta^{13}C_{atm} - \delta^{13}C_R}{(1 - \delta^{18}O_{atm})}
\]

where Δδ¹³C is the photosynthetic discrimination against ¹³C in the atmosphere (‰), δ¹³C_atm is the carbon isotope composition of the atmospheric CO₂, c_a is the mean annual atmospheric CO₂ concentration, a is the fractionation during CO₂ diffusion through stomata (4.4‰), and b is the fractionation during carboxylation (27‰). We obtained annual values of c_a and δ¹³C_atm from Francey et al. (1999), McCarroll and Loader (2004), and McCarroll et al. (2009). The calculation of WUEi removes the effects of an increasing atmospheric CO₂ concentration and declining δ¹³C of atmospheric CO₂ due to fossil fuel combustion on the isotope ratios of annual growth rings. Therefore, WUEi values were used for all subsequent statistical analyses.

**Estimating population-level vulnerability to drought**

To quantify the population-level annual growth response to each target drought period, we estimated the drought resistance (D_rs) and resilience (D_rl) of trees within each plot using:

\[
D_{rs} = \frac{BAI_D}{BAI_{pre}}
\]

\[
D_{rl} = \frac{BAI_{post}}{BAI_{pre}}
\]

where D_rs values <1 indicate lower (and >1 indicate higher) population-level annual growth rates during drought years (BAI_D) relative to pre-drought years (BAI_pre; Sensu D’Amato et al. 2013). Similarly, D_rl indicates whether population growth rates following drought events (BAI_post) were lower (<1) or higher (>1) relative to pre-drought years (BAI_pre; sensu D’Amato et al. 2013).
drought periods. To extend beyond the 19-month preconditioning period yet avoid overlap between drought periods, we defined pre-drought and post-drought years as the two years immediately prior and after a drought event.

To quantify the physiological response of trees to drought, we calculated the change in WUE$_i$ and $\delta^{18}$O$_R$, defined as the increase in mean WUE$_i$ and $\delta^{18}$O$_R$ ($\%$), respectively, during dry years relative to wet years within each pooled sample. During drought stress, leaf stomatal conductance is affected to a greater extent than assimilation, resulting in an increase in $\delta^{13}$C$_R$ and thus higher WUE$_i$ values during dry versus wet years (Ehleringer and Cooper 1988). Concurrently high $\delta^{18}$O$_R$ values during dry versus wet years further suggest reduced stomatal conductance in response to water stress (Ehleringer and Dawson 1992).

Forest floor and mineral soil nitrogen
We quantified changes in forest floor mass, N concentration and C/N ratio as well as total (TN) and inorganic N (IN) content of mineral soil by collecting soil samples from one replicate plot per treatment per block. To quantify soil IN content, we collected samples of Oa and mineral soil from three and six random locations, respectively, per plot in June 2008. Mineral soil was collected in 10-cm increments to 80 cm depth using a 5 cm diameter corer. Using standard KCl extraction and NH$_3$ and NO$_3$ analysis methods (see Appendix S1), we calculated inorganic soil N content as the sum of NH$_4^+$ and NO$_3^-$ concentrations (inclusive NO$_2^-$) in mg N per kg dry soil. To quantify litter layer and mineral soil TN content and C/N, we installed a 30 cm diameter template at eight sampling locations per plot in June 2009. We collected undecomposed and moderately decomposed forest floor litter layers (Oi and Oe horizons) and the decomposed (humus) layer (Oa horizon) separately, followed by mineral soil sampling in increments (0–5, 5–10, 10–20, and 20–30 cm depth) using a 5 cm diameter corer. We used standard methodology to homogenize subsamples prior to elemental analysis of TN and TC concentrations ($\%$; see Appendix S1).

Data analysis
We used two modeling approaches to assess the effect of fire on the growth response of adult oaks to drought. First, we analyzed temporal trends, both long-term (1951–2015) and recent (1985–2015), in annual BAI for each individual $i$ as a function of climate and fire treatment using a linear mixed model with a first-order autoregressive covariance structure. Among a total of eight climate variables tested, PET (19-month) was the most strongly correlated with standardized radial growth based on bootstrapping (Appendix S1: Fig. S1) and thus was used for all statistical analyses. Log-transformed BAI, was modeled as a function of PET (19-month), dbh$\_i$, age$_i$, species$_i$, year, fire treatment, years since last burn, and block. We excluded highly correlated variables (rho $\geq 0.5$) from the same model. Moreover, due to tree age and year being highly correlated, we chose to use only year in all further analyses based on year outperforming tree age in model comparisons. All continuous predictors, including year, were mean-centered to reduce collinearity. We included two- and three-way interactions between PET, fire treatment, years since last burn and species. A random intercept and slope were specified such that the intercept and effect of year on BAI, were allowed to vary by treeID$_i$, nested within plot. There were no data available on years since last burn for unburned controls, so we assigned the median years since last burn from the periodic and annual treatments (1.5 yr) to the unburned controls, similar to Sohn et al. (2016a). Therefore, the parameter estimates for years since last burn primarily represent the effect of treatment timing in periodic (0–3 yr) and annual (0 yr) burned plots relative to the median treatment timing (1.5 yr). Because all variables in the final models were statistically significant, we used the standardized parameter estimates from each model to understand the sensitivity of annual BAI to changes in relative values of each predictor variable. Standardized parameter estimates were derived from models fit after re-scaling all continuous predictor variables to a mean of zero and standard deviation of one.

Second, to examine how fire may influence drought response through reductions in density-dependent competition, we used separate linear mixed models to analyze the (1) resistance ($D_r$) and resilience ($D_{rl}$) of annual BAI for each individual and the (2) change in WUE$_i$ and $\delta^{18}$O between targeted wet and dry years as a function of...
of plot BA (m²/ha) or stem density (stems/ha), cumulative number of burns, species, and the relative change in PET (19-month) during each drought event. The change in PET was defined as the PET of the drought year minus the mean PET two years prior ($D_{rs}$ model) or after the drought year ($D_{rl}$ model) or between the target dry and wet years (WUE$_i$ and $\delta^{18}O$ models). We tested two-way interactions between BA, PET change, number of burns, and species. The sample pool nested within plot and drought period were included as random intercepts. Past data on plot basal area and stem density from 1950 (pre-treatment), 1964, and 2013 originated from Knapp et al. (2017a).

Bootstrapped correlations were used to examine the relationships between WUE$_i$ or $\delta^{18}O$R and PET or standardized radial growth across fire treatments (see Appendix S1). Finally, we used separate linear mixed models to estimate the effect of fire treatment on the mass, N content and C/N ratio of the litter layer (Oi + Oe), and the concentrations of IN and TN for the Oa layer and each mineral soil depth increment. Plot nested within block was included as a random intercept. Litter layer mass and soil inorganic N concentration were log transformed to achieve normality. All mixed models were performed in R version 3.6.2 (R Core Team 2019) using the packages nlme (Pinheiro et al. 2017) and lmer4 (Bates et al. 2015).

**RESULTS**

**Climate–growth relationship across fire treatments**

Tree-level total BAI increased with tree diameter and declined with calendar year and PET.

Table 2. Raw and standardized parameter estimates from linear mixed models predicting log annual basal area increment (BAI, cm²/yr) of adult trees (≥ 10 cm dbh) across unburned controls, annual, and periodic burn (every four years) treatments during (a) the entire experiment period (1951–2015) and (b) the most recent 30 yr (1985–2015).

| Parameter | Fixed effects | Random effects |
|-----------|---------------|----------------|
|           | Estimate | SE | Standardized estimate | P (> |t|) | Group intercept | Variation | SD |
| a) Annual BAI (1951–2015) | | | | | | | | |
| Intercept | 30.03 | 1.82 | 0.0 | <0.001 | plot | 0.05 | 0.23 |
| PET | -0.02 | 0.001 | -0.115 | <0.001 | treeID:plot | 0.44 | 0.66 |
| Year | -0.01 | 0.001 | -0.416 | <0.001 | residual | 0.14 | 0.37 |
| Dbh | 0.08 | 0.003 | 1.216 | <0.001 | | | |
| Block | 0.08 | 0.18 | 0.665 | 0.66 | | | |
| FirePeriodic | -0.23 | 0.22 | -0.171 | 0.33 | | | |
| FireAnnual | -0.15 | 0.22 | -0.114 | 0.50 | | | |
| Yrs since last burn | 0.01 | 0.003 | 0.012 | 0.0047 | | | |
| FirePeriodic × PET | 0.005 | 0.002 | 0.016 | 0.0062 | | | |
| FireAnnual × PET | -0.001 | 0.002 | -0.018 | 0.52 | | | |
| Yrs since last burn × PET | -0.003 | 0.001 | -0.019 | <0.001 | | | |
| b) Annual BAI (1985–2015) | | | | | | | | |
| Intercept | 11.04 | 2.27 | 0.0 | <0.001 | plot | 0.02 | 0.14 |
| PET | -0.01 | 0.002 | -0.068 | <0.001 | treeID:plot | 0.27 | 0.52 |
| Year | -0.004 | 0.001 | -0.065 | <0.001 | residual | 0.08 | 0.28 |
| Dbh | 0.04 | 0.004 | 0.682 | <0.001 | | | |
| Block | 0.12 | 0.13 | 0.095 | 0.38 | | | |
| Species Q. stellata | -0.07 | 0.11 | -0.054 | 0.54 | | | |
| FirePeriodic | -0.18 | 0.15 | -0.138 | 0.29 | | | |
| FireAnnual | -0.13 | 0.15 | -0.102 | 0.40 | | | |
| Yrs since last burn | 0.02 | 0.004 | 0.030 | <0.001 | | | |
| Species Q. stellata × PET | 0.01 | 0.002 | 0.022 | 0.0307 | | | |
| FirePeriodic × PET | 0.005 | 0.002 | 0.011 | 0.0439 | | | |
| FireAnnual × PET | -0.002 | 0.002 | -0.001 | 0.48 | | | |

Notes: For the period 1951–2015, number of observations = 10,752; plot = 12; plot, treeID = 173. For the period 1985–2015, number of observations = 5,310; plot = 12; plot, treeID = 173.
over the study period (1950–2015) for both species ($P < 0.001$; Table 2a, Fig. 1). While tree-level and cumulative BAI were reduced in both annually and periodically burned plots relative to controls (Appendix S3: Fig. S1), this effect was driven by smaller mean tree size in annually burned plots (Table 1; Appendix S2: Fig. S2). After controlling for the main, dominant effects of tree diameter, calendar year, and climate, we found a significant interaction between periodic fire and PET such that periodic burns significantly reduced BAI of both species during wet, favorable periods of low PET (periodic fire $\times$ PET: $P = 0.01$; Table 2a). Although the interactive effect of periodic fire and PET on tree growth was small relative to the influence of tree diameter, calendar year, and climate (see standardized estimates in Table 2), periodic burning reduced annual growth by 9.6% ($\pm 8\%$ CI) relative to controls under low PET while having more variable effects on growth under high PET ($-6.1\% \pm 9\%$). Furthermore, there was a significant interaction between years since last burn and PET such that more recently burned plots experienced a greater reduction in growth, especially during wet, favorable periods (yrs since last burn $\times$ PET: $P < 0.001$). There were no main or interactive effects of species on long-term growth.

Treatment effects on tree-level total BAI did not vary over time (annual or periodic fire $\times$ year: $P > 0.05$). Examining only the most recent 30 yr of growth (1985–2015), we found patterns similar to that of the entire study period, with tree-level total BAI of both species varying with calendar year, tree diameter, PET, and the interaction between PET and periodic fires (periodic fire $\times$ PET: $P = 0.04$; Table 2b, Fig. 1). Consistent with the trends for the entire study period, annual burns had no effect on growth (Table 2b, Fig. 1). Years since last burn was associated with increased growth rates ($P < 0.001$), but unlike for the entire study period, there was no interaction between years since last burn and PET. During this most recent 30-year period, there was also a significant interaction between species and PET such that declines in growth during drought conditions were significantly smaller for Q. stellata than Q. falcata (species $\times$ PET: $P = 0.03$; Fig. 1b, c).

**Resistance and resilience of growth to drought across fire treatments**

There was no relationship between plot BA, PET change, or cumulative number of burns on drought resistance ($D_{rs}$) or resilience ($D_{rl}$) of annual BAI (Fig. 2a, b; Appendix S3: Table S1). The vulnerability of growth to drought varied by species, with Q. stellata maintaining both greater drought resistance ($P < 0.01$) and resilience ($P < 0.05$) than Q. falcata. Similarly, there were no observed relationships between $D_{rs}$, $D_{rl}$, and tree density (data not shown).

**WUE$_i$ and $\delta^{18}O$ of growth rings across fire treatments**

Standardized radial growth was significantly negatively correlated with the water stress signal Fig. 2. Mean ($\pm$ SE) plot-level (a) drought resistance ($D_{rs}$), (b) drought resilience ($D_{rl}$), (c) change in calculated intrinsic water use efficiency (WUE$_i$), and (d) change in oxygen isotopic composition of radial growth rings ($\delta^{18}O_4$) between dry and wet years as a function of plot basal area (m$^2$/ha) during each targeted drought event. Dashed lines denote where $D_{rs}$, $D_{rl}$, WUE$_i$, and $\delta^{18}O$ are equal across wet and dry years. Sample sizes are summarized in Appendix S2: Tables S1 and S2.
of δ$_{18}$O$_R$ ($r = -0.48$, $P < 0.001$ at 95% CI, $n = 60$) but not WUE$_i$ ($r = -0.17$, $P > 0.05$ at 95% CI, $n = 60$; Appendix S3: Fig. S2). WUE$_i$ and δ$_{18}$O$_R$ were significantly positively correlated with each other ($r = 0.44$, $P = 0.002$ at 95% CI, $n = 60$) and marginally positively correlated with PET ($r = 0.47$, $P = 0.09$, $n = 10$; $r = 0.50$, $P = 0.08$, $n = 10$, respectively; Appendix S3: Fig. S3).

WUE$_i$ and δ$_{18}$O$_R$ showed a greater change between dry and wet years during more severe drought periods (PET change: $P = 0.053$; $P < 0.001$, respectively). After accounting for this effect, we found no relationship between plot BA and change in WUE$_i$ or δ$_{18}$O$_R$ for either species ($P > 0.05$; Fig. 2c, d; Appendix S3: Table S2). As treatment plots experienced more cumulative burns over time, trees showed significantly less change in WUE$_i$ (but not δ$_{18}$O$_R$) between dry and wet years ($P = 0.018$). Change in WUE$_i$ did not differ between study species, but Q. stellata showed significantly less change in δ$_{18}$O$_R$ between dry and wet years than Q. falcata ($P < 0.01$) (Appendix S3: Table S2). No relationship was found between tree density and the change in isotopic composition (data not shown).

**Long-term effects of fire on forest floor and soil N**

Annual but not periodic burning significantly reduced the mass of the litter layer (Oi + Oe), with annually burned plots containing 67% (±54% CI) less litter layer mass than the unburned control ($P = 0.04$; Appendix S3: Fig. S4a). Litter layer mass did not differ between annual and periodic treatments ($P = 0.16$). Compared to controls, litter layer C/N ratio was significantly greater in annually ($P = 0.03$), but not periodically burned plots ($P > 0.05$; Appendix S3: Fig. S4b). Litter layer C/N ratio did not differ between annual and periodic burning treatments ($P > 0.05$).

Total N concentration of the litter layer did not differ among treatments ($P > 0.05$), although there was a trend for lower total N concentration in annually burned plots (Fig. 3a). Scaling by differences in litter layer mass, we found that litter layer N pools were 77% (±89% CI) smaller in annually burned plots relative to the control ($P = 0.04$; Appendix S3: Fig. S4c). Periodic burning had no effect on litter layer N mass ($P > 0.05$), relative to the control.

Total N concentrations did not differ by treatment in the Oa or any of the mineral soil depths (0–30 cm; Fig. 3a). Soil inorganic N concentrations also did not vary across the treatments, and

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**Fig. 3.** Mean (± SE) (a) concentrations of total nitrogen (%) in litter layer (Oi + Oe horizons), humus (Oa horizon) and mineral soil by depth (0–30 cm), and (b) content of soil inorganic N (mg NH$_4$–N + NO$_3$–N/kg dry soil) in humus (Oa horizon) and mineral soil by depth (0–80 cm). Inorganic soil N concentration data were collected in June 2008; litter layer and soil N content data were collected in June 2009.
there was no interaction between treatment and soil depth, including the Oa horizon ($P > 0.05$; Fig. 3b).

**DISCUSSION**

We leveraged a unique, long-term (65 yr) fire manipulation experiment to examine the interactive effects of climate and fire frequency on annual growth rates of two *Quercus* spp. To our knowledge, this is one of the only stand-level experiments in hardwood forests that has manipulated fire frequency for more than a few decades. This study thus provides rare insights into how repeat burning can alter tree response to climate change.

We found periodic, but not annual, fires moderated the response of tree growth to climate. Contrary to our predictions, this effect was not due to greater drought resistance or resilience, but rather, due to significantly slower growth of periodically burned trees during wet periods favorable for growth. Periodic fires reduced radial growth rates by approximately 10% per year on average under wet conditions, an effect of similar magnitude to that of climate, where radial growth declined 8–12% during dry, high PET years relative to years of average PET. The interactive effect of periodic burning and climate on growth was consistent over time and the magnitude of effects did not strengthen over time. Our results therefore suggest that recurring fire can have considerable, negative impacts on long-term tree growth and that the magnitude of effects is contingent upon fire frequency.

Our finding, that declines in tree growth were greatest immediately after fire, is consistent with results from several past studies conducted in needleleaf forests (Ford et al. 2010, Ames et al. 2015, Valor et al. 2015). Furthermore, we show that time since fire interacts with climate such that recent burns had more negative effects on growth during wet years (Table 2), similar to the climate-contingent effects of fire timing on *Pinus* spp. growth over a 20-year period found by Ames et al. (2015). After accounting for the timing of disturbance, we find that periodic, but not annual, fires reduced tree growth during wet years of low PET. Similarly, Ford et al. (2010) found fires with longer return intervals (5–7 yr) had a larger negative effect on *Pinus palustris* growth the year of the burn than shorter interval fires (1–2 yr) over a 25-yr study period. Our results diverge significantly from these past studies, however, in that we found the suppression of tree growth under periodic fires was persistent over our entire study period (1951–2015).

**Effect of fire-driven reductions in forest density on tree drought resistance and resilience**

We found minimal support for our hypothesis that long-term, fire-driven reductions in tree density minimize drought stress in adult *Quercus* (H1). Overall, high WUEi and δ18O_R, and low radial growth during dry years indicate that trees across all treatments experienced lower stomatal conductance and constrained photosynthetic activity and growth during drought (Table 2; Appendix S3: Figs S2 and S3). Across four severe drought periods (1953–1954, 1964, 2007, and 2012), we found no relationship between drought resistance and resilience in annual growth and reductions in plot basal area in fire-treated plots (Fig. 2a, b). Although we found the cumulative number of burns was associated with significantly less change in WUEi (but not δ18O_R) between dry and wet years (Appendix S3: Table S2), our carbon and oxygen isotope results otherwise suggest no relationship between plot basal area and drought stress (Fig. 2c, d).

Results from this fire manipulation study contrast with recent studies of mechanical thinning treatments in needleleaf forests that found reductions in tree density at least temporarily improve drought resistance and resilience (D’Amato et al. 2013, Sohn et al. 2016a, Bottero et al. 2017). These different findings may be due to several factors. First, the alleviation of water stress is likely highly contingent upon the magnitude of stand disturbance, which can differ substantially between thinning and fire. Past studies found heavy (50–80%) reductions in basal area were necessary to improve forest drought resistance and resilience relative to controls (D’Amato et al. 2013, Bottero et al. 2017). By comparison, 63 yr of burning caused only modest reductions in basal area (11–26%). Annual and periodic fires at the study site have, however, reduced mean LAI by 34–44%, respectively, relative to controls (Knapp et al. 2015). Given LAI is a major determinant of plant water demand (Jump et al. 2017), we
would expect the relatively large reduction in LAI with fire to have influenced drought resistance and resilience. Instead, our findings suggest factors other than disturbance severity may be responsible for the lack of an effect on drought resistance and resilience.

Second, although both thinning and repeated prescribed burning can reduce stand density, they differ both in the rate at which the reduction occurs and the length of time between disturbances. Whereas thinning results in an immediate loss of competitors followed by recovery, frequent burning results in a gradual loss of competitors by killing trees and also reducing or filtering recruitment (Knapp et al. 2015). This difference in the rate of competitor loss is important because trees can quickly acclimate to competitive release through compensatory gains in their size, a response that can increase stand-level transpiration and water demand and counter or even negate the positive effects of disturbance on water availability (McDowell et al. 2006). Even for severe thinning treatments, the benefits for drought resistance and recovery often decline with time since treatment due to these compensatory gains (D’Amato et al. 2013, Sohn et al. 2016a, b). Therefore, the slow loss of competitors with repeat fires may never result in an observable benefit to the drought resistance or recovery of adult trees.

Our results support past studies in eastern North America that suggest oak species belonging to the white oak clade are generally more drought tolerant than those in the red oak clade (Huddell and Pallardy 1996, Klockow et al. 2018). In our study, *Q. stellata* (section *Leucobalanus*) maintained higher growth rates than *Q. falcata* (section *Erythrobalan us*) during dry years, but only during the most recent 30 yr, and *Q. stellata* had higher drought resistance and resilience in growth than *Q. falcata*. Patterns from isotopic indicators of drought stress were mixed, with the change in WUE, between dry and wet years similar between species, while *Q. stellata* showed significantly less change in δ18O than *Q. falcata*. Despite these interspecific differences in overall drought tolerance, we found that neither species showed improved drought response to fire-driven reduction in competition. This lack of a fire-driven, density-dependent drought response in Quercus spp. may be due to their deep root systems, which may help minimize intra- and interspecific competition for soil water during drought. Oaks are among the deepest rooted tree species in North America (Gale and Grigal 1987, Abrams 1990), and in studies conducted in semiarid systems, they have been observed shifting to deeper water sources during dry periods in order to avoid desiccation (del Castillo et al. 2016). The ability of *Quercus* to access a deeper and more reliable water supply may minimize the influence of intra- and interspecific competition for soil water on drought vulnerability relative to other, less drought-tolerant species (Klos et al. 2009, Martín-Gómez et al. 2017; but see Voelker et al. 2008). Consequently, vapor pressure deficit (VPD) can be a better predictor of drought-induced stress and mortality in *Quercus* than soil water, especially during moderate drought events (Voelker et al. 2014, Gu et al. 2015). Although rooting depth may help explain the contrast between our results and the majority of thinning studies that focus on more shallow-rooted coniferous tree species (Sohn et al. 2016b), the limited number of studies on *Quercus* spp., all in Europe, has found short-term, positive effects of thinning on drought performance (Corcuera et al. 2006, Moreno and Cubera 2008, Rodriguez-Calcerrada et al. 2011). More studies on a wide range of species are needed to better identify and generalize patterns.

**Contribution of post-fire losses of soil N to fire-driven declines in tree growth**

We found no evidence that the observed long-term, negative impacts of periodic fire on tree growth are associated with soil N loss (H2). Instead, we observed reductions in litter biomass and litter N under annual, rather than periodic, burning (Appendix S3: Fig. S4). Furthermore, soil samples collected after almost 60 yr of treatment showed total soil N and inorganic N concentrations were similar among treatments (Fig. 3). Although these results suggest factors other than N are responsible for growth declines under periodic fires, we emphasize that our methods may not have been sensitive enough to detect effects on N availability. Specifically, one-time measurements of total and inorganic N concentrations may misrepresent long-term patterns in N supply and greater replication and/or more sampling dates may be required to detect
change. Therefore, we cannot exclude the possibility that fire-driven loss of soil N may be driving the effects of periodic burning on tree growth.

In contrast to our results, earlier studies on soil N availability at this study site suggest that increased N limitation with burning may have contributed to slower growth in the past. Specifically, in a study conducted after 43 yr of treatment, annual and periodic burning reduced total soil N concentrations (0–15 cm depth) by 54–60% relative to controls (Eivazi and Bayan 1996). Similarly, in a study conducted after 34 yr of treatment, Vance and Henderson (1984) found annual and periodic burning reduced NH$_4^+$ availability by 30–44% and N mineralization rates by 17–30% relative to controls.

**Other possible factors contributing to fire-driven declines in tree growth**

Although past observed reductions in N with burning may have contributed to reduced growth in annually and periodically burned plots, injury from fire may be an especially important driver of growth declines under periodic burning. Injury from surface fires can result from direct combustion of plant tissue and heat transfer through radiation, conduction, and convection. Past studies on fire injury have often focused on conifer mortality, where crown injury is often implicated as the primary cause (Hood et al. 2018). Unlike wildfires in coniferous forests, prescribed burning in temperate deciduous forests typically produces lower-intensity, surface fires that are applied in the dormant season, when tree crowns lack foliage. Therefore, injury to stem and root tissue is a more likely contributor to growth declines in deciduous oak species (Regelbrugge and Smith 1994, Keyser et al. 2018), which lack an insulating layer of needles on the forest floor and the thick, protective bark found in many conifer tree species (e.g., *Pinus ponderosa*). The vulnerability of oaks to stem injury from fire is also evident in adaptations such as a greater allocation of bark observed at the stem base of burned than unburned oaks (Graves et al. 2014, Hammond et al. 2015).

Past and present results from our study site support cambial and/or root injury as a possible cause of the observed declines in growth with periodic but not annual fires. First, at the same plots as the present study, Knapp et al. (2017b) found the incidence of scarring on the lower portion of adult tree boles was 5% in annual burned plots and 55% in periodic burned plots. The higher incidence of scarring in periodic plots is likely due to the longer return intervals, higher fuel accumulation, and understory vegetation cover (Knapp et al. 2015), and therefore greater fire intensity and probability of cambial injury under periodic than annual burns (Peterson and Reich 2001, Hutchinson et al. 2005). Considering that fire scar wounds require 1–24 yr to heal in *Q. alba* (Stambaugh et al. 2017), periodic fires were likely frequent enough to re-expose cambial tissue to lethal levels of heat prior to wound closure. The resulting cambial necrosis can reduce xylem conductivity and photosynthetic rates by preventing water and nutrients from reaching the tree canopy (Dickinson and Johnson 2004, Sword Sayer and Haywood 2006, Michaletz and Johnson 2007). Second, although we found annual, not periodic fires reduced litter layer mass relative to unburned controls (Appendix S3: Fig. S4a), the greater intensity of periodic burns may result in greater conduction of heat to the soil and higher rates of root injury and loss of functions important for growth (e.g., root non-structural carbohydrates; Varner et al. 2009).

We found periodic fires caused growth declines during wet years for both study species, *Q. falcata* and *Q. stellata*, suggesting the mechanism responsible for fire-driven reductions in growth extends beyond potential species-specific differences in fire tolerance. Furthermore, Ames et al. (2015) reported fire-driven reductions in the growth of longleaf pine (*Pinus palustris*), suggesting that even species considered highly resistant to fire-driven mortality can be susceptible to fire-driven declines in growth. Therefore, research is needed on injury as a potential mechanism of fire-driven growth declines in deciduous broadleaf trees and functional traits that may moderate species’ response.

**Limitations**

Long-term field experiments can be immensely valuable in addressing contemporary ecological questions, with the caveat that these experiments were often originally designed to address different questions. Therefore, care must be taken to consider possible ways that our findings could...
be confounded by limitations of the experimental design. In this experiment, periodic fires were not prescribed during the same year across the two blocks, resulting in the staggered application of periodic burns. Given fire-driven declines in growth are greatest shortly after fire, we speculate that the staggered treatments introduced noise into the long-term growth series as well as calculations of drought resistance and resilience in periodic burn plots. However, our analysis included several steps intended to minimize bias that may have been introduced. First, we ran separate bootstrap correlations and confirmed that PET was well-correlated with annual growth regardless of block or treatment. Second, we incorporated time since fire into our climate-growth models to help account for effects of staggered periodic burns on annual radial growth. Finally, we found general agreement among complementary lines of evidence—annual radial growth and carbon and oxygen isotopes—that the resistance and resilience of trees to multiple drought events was unaffected by fire treatment. Therefore, although caution should be taken when interpreting and extrapolating results from this case study, we argue that our conclusions are robust to the staggered application of periodic burns in this experiment.

**Conclusions**

Over approximately 65 yr of increased fire frequency, we found fire-driven reductions in stem density had little to no effect on the drought resistance and resilience of adult *Quercus* spp. trees. Instead, we found periodic burning reduced annual growth rates by 9.6% during wet periods favorable for growth, an effect that was consistent over time. We did not find corresponding reductions in N availability with fire, suggesting that growth declines were due to a combination of other factors, such as past, transient reductions in soil N or accumulated cambium and root damage sustained from the long-term fire treatments. Regardless of the mechanisms suppressing growth (e.g., N limitation, fire injury), our findings suggest that the observed reduction in annual growth rates during favorable periods offset any expected gains in growth due to reductions in density-dependent competition. Furthermore, the observed declines in annual growth rates combined with stand-level reductions in tree density with periodic fires underscore the important impacts of fire frequency on forest productivity and carbon sink potential. Overall, our results suggest that fire has very different effects than thinning on forest drought response, and its distinct effects must be considered prior to using it as a management strategy for increasing the adaptive capacity of forests. Further research that involves cooperation between scientists and forest managers is needed to better evaluate the efficacy of different management actions for mitigating forest vulnerability to climate change, especially the inherent trade-offs involved with their application.

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**LITERATURE CITED**

Abrams, M. D. 1990. Adaptations and responses to drought in *Quercus* species of North America. Tree Physiology 7:227–238.

Ames, G. M., D. L. Vineyard, S. M. Anderson, and J. P. Wright. 2015. Annual growth in longleaf (*Pinus palustris*) and pond pine (*P. serotina*) in the Sandhills of North Carolina is driven by interactions between fire and climate. Forest Ecology and Management 340:1–8.

Anderegg, W. R. L., C. Schwalm, F. Biondi, J. J. Camarero, G. Koch, M. Litvak, K. Ogle, J. D. Shaw, E. Shevliakova, A. P. Williams, A. Wolf, E. Ziaco, and S. Pacala. 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science 349:528–532.

Barbour, M. M. 2007. Stable oxygen isotope composition of plant tissue: a review. Functional Plant Biology 34:83.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–51.
Biondi, F. 1999. Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. Ecological Applications 9:216–227.

Bottero, A., A. W. D’Amato, B. J. Palik, J. B. Bradford, S. Fraver, M. A. Battaglia, and L. A. Asherin. 2017. Density-dependent vulnerability of forest ecosystems to drought. Journal of Applied Ecology 54:1605–1614.

Bradford, J. B., and D. M. Bell. 2017. A window of opportunity for climate-change adaptation: easing tree mortality by reducing forest basal area. Frontiers in Ecology and the Environment 15:11–17.

Bréda, N., R. Huc, A. Granier, and E. Dreyer. 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Annals of Forest Science 63:625–644.

Bunn, A. G. 2008. A dendrochronology program library in R (dpIR). Dendrochronologia 26:115–124. http://doi.org/10.1016/j.dendro.2008.01.002

Carter, M. C., and C. Darwin Foster. 2004. Prescribed burning and productivity in southern pine forests: a review. Forest Ecology and Management 191:93–109.

Choat, B., et al. 2012. Global convergence in the vulnerability of forests to drought. Nature 491:752–755.

Cook, E. R., and L. A. Kairiukstis. 1990. Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Córcuera, L., J. J. Camarero, S. Sisó, and E. Gil-Pelegrín. 2006. Radial-growth and wood-anatomical changes in overaged Quercus pyrenaica coppice stands: functional responses in a new Mediterranean landscape. Trees 20:91–98.

D’Amato, A. W., J. B. Bradford, S. Fraver, and B. J. Palik. 2013. Effects of thinning on drought vulnerability and climate response in northern temperate forest ecosystems. Ecological Applications 23:1735–1742.

D’Orangeville, L., et al. 2018. Drought timing and local climate determine the sensitivity of eastern temperate forests to drought. Global Change Biology 24:2339–2351.

DeBano, L. F., D. G. Neary, and P. F. Flomliott. 1998. Fire effects on ecosystems. John Wiley, New York, New York, USA.

del Castillo, J., C. Comas, J. Voltas, and J. P. Ferrio. 2016. Dynamics of competition over water in a mixed oak-pine Mediterranean forest: spatio-temporal and physiological components. Forest Ecology and Management 382:214–224.

Dickinson, M. B., and E. A. Johnson. 2004. Temperature-dependent rate models of vascular cambium cell mortality. Canadian Journal of Forest Research 34:546–559.

Ehleringer, J. R., and T. A. Cooper. 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. Oecologia 76:562–566.

Ehleringer, J. R., and T. E. Dawson. 1992. Water uptake by plants: perspectives from stable isotope composition. Plant, Cell and Environment 15:1073–1082.

Eivazi, F., and M. R. Bayan. 1996. Effects of long-term prescribed burning on the activity of select soil enzymes in an oak-hickory forest. Canadian Journal of Forest Research 26:1799–1804.

Farquhar, G. D., J. R. Ehleringer, and K. T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology 40:503–537.

Farquhar, G., M. O’Leary, and J. Berry. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Functional Plant Biology 9:121.

Ford, C. R., E. S. Minor, and G. A. Fox. 2010. Long-term effects of fire and fire-return interval on population structure and growth of longleaf pine (Pinus palustris). Canadian Journal of Forest Research 40:1410–1420.

Francey, R. J., C. E. Allison, D. M. Etheridge, C. M. Trudinger, I. G. Enting, M. Leuenberger, R. L. Langenfelds, E. Michel, and L. P. Steele. 1999. A 1000-year high precision record of δ13C in atmospheric CO2. Tellus B: Chemical and Physical Meteorology 51:170–193.

Gale, M. R., and D. F. Grigal. 1987. Vertical root distributions of northern tree species in relation to successional status. Canadian Journal of Forest Research 17:829–834.

Granier, A., N. Bréda, P. Biron, and S. Villette. 1999. A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. Ecological Modelling 116:269–283.

Graves, S. J., S. W. Rifai, and F. E. Putz. 2014. Outer bark thickness decreases more with height on stems of fire-resistant than fire-sensitive Floridian oaks (Quercus spp.; Fagaceae). American Journal of Botany 101:2183–2188.

Grossiord, C., et al. 2014. Tree diversity does not always improve resistance of forest ecosystems to drought. Proceedings of the National Academy of Sciences 111:14812–14815.

Gu, L., S. G. Pallardy, K. P. Hosman, and Y. Sun. 2015. Drought-influenced mortality of tree species with different predawn leaf water dynamics in a decade-long study of a central US forest. Biogeosciences 12:2831–2845.

Hammond, D. H., J. M. Varner, J. S. Kush, and Z. Fan. 2015. Contrasting sapling bark allocation of five
southeastern USA hardwood tree species in a fire prone ecosystem. Ecosphere 6:112.
Holmes, R. L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43:69–78.
Hood, S. M., J. M. Varner, P. van Mantgem, and C. A. Cansler. 2018. Fire and tree death: understanding and improving modeling of fire-induced tree mortality. Environmental Research Letters 13:113004.
Huddle, J. A., and S. G. Pallardy. 1996. Effects of long-term annual and periodic burning on tree survival and growth in a Missouri Ozark oak-hickory forest. Forest Ecology and Management 82:1–9.
Hutchinson, T. F., E. K. Sutherland, and D. A. Yaussy. 2009. Drought impact on forest growth and mortality. Environmental Research Letters 4:344:95–109.
Knapp, B. O., K. Stephan, and J. A. Hubbart. 2015. Structure and composition of an oak-hickory forest after over 60 years of repeated prescribed burning in Missouri, U.S.A. Forest Ecology and Management 344:95–109.
Knapp, B. O., M. A. Hullinger, and J. M. Kabrick. 2015. Effects of repeated prescribed fires on the structure, composition, and regeneration of mixed-oak forests in Ohio. Forest Ecology and Management 218:210–228.
Klos, R. J., G. G. Wang, W. L. Bauerle, and J. R. Rieck. 2017. Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. Global Change Biology 23:3742–3757.
Knapp, B. O., K. Stephan, and J. A. Hubbart. 2018. Short-term stem mortality of 10 deciduous broadleaved species following prescribed burning in upland forests of the Southern US. International Journal of Wildland Fire 27:42.
Knapp, B. O., M. A. Hullinger, and J. M. Kabrick. 2017a. Effects of fire frequency on long-term development of an oak-hickory forest in Missouri, U.S.A. Forest Ecology and Management 387:19–29.
Knapp, B. O., J. M. Marschall, and M. C. Stambaugh. 2017b. Effects of long-term prescribed burning on timber value in hardwood forests of the Missouri Ozarks. Pages 304–313 in General Technical Report NRS-P-167. U.S. Department of Agriculture, Forest Service, Newtown Square, PA.
Loader, N. J., I. Robertson, and D. McCarroll. 2003. Comparison of stable carbon isotope ratios in the whole wood, cellulose and lignin of oak tree-rings. Palaeogeography, Palaeoclimatology, Palaeoecology 196:395–407.
Martin-Gómez, P., M. Aguilera, J. P. Pelegrín, and J. P. Ferrio. 2017. Contrasting eco-physiological strategies related to drought: the case of a mixed stand of Scots pine (Pinus sylvestris) and a submediterranean oak (Quercus subpyrenaica). Tree Physiology 37:1478–1492.
McCarroll, D., M. H. Gagen, N. J. Loader, I. Robertson, K. J. Anchukaitis, S. Los, G. H. F. Young, R. Jalkanen, A. Kirchhefer, and J. S. Waterhouse. 2009. Correction of tree ring stable carbon isotope chronologies for changes in the carbon dioxide content of the atmosphere. Geochimica Et Cosmochimica Acta 73:1539–1547.
McCarroll, D., and N. J. Loader. 2004. Stable isotopes in tree rings. Quaternary Science Reviews 23:771–801.
McDowell, N. G., H. D. Adams, J. D. Bailey, M. Hess, and T. E. Kolb. 2006. Homeostatic maintenance of ponderosa pine gas exchange in response to stand density changes. Ecological Applications 16:1164–1182.
Michaletz, S. T., and E. A. Johnson. 2007. How forest fires kill trees: a review of the fundamental biophysical processes. Scandinavian Journal of Forest Research 22:500–515.
Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17:2145–2151.
Moreno, G., and E. Cubera. 2008. Impact of stand density on water status and leaf gas exchange in Quercus ilex. Forest Ecology and Management 254:74–84.
Offermann, C., J. P. Ferrio, J. Holst, R. Grote, R. Siegwolf, Z. Kayler, and A. Gessler. 2011. The long way down—are carbon and oxygen isotope signals in the tree ring uncoupled from canopy physiological processes? Tree Physiology 31:1088–1102.
Pan, Y., et al. 2011. A large and persistent carbon sink in the world’s forests. Science 333:988–993.
Pellegrini, A. F. A., A. Ahlström, S. E. Hobbie, P. B. Reich, L. P. Nieradzik, A. C. Staver, B. C. Scharenbroch, A. Jumpponen, W. R. L. Anderegg, J. T. Randerson, and R. B. Jackson. 2018. Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. Nature 553:194–198.
Peterson, D. W., and P. B. Reich. 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. Ecological Applications 11:914–927.
DATA AVAILABILITY STATEMENT

All tree radial growth and isotopic composition data used in this article are publicly available in the Illinois Data Bank (https://doi.org/10.13012/B2IDB-6771049_V1).

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3287/full