



## RESEARCH ARTICLE

# Fire increases drought vulnerability of *Quercus alba* juveniles by altering forest microclimate and nitrogen availability

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**Funding information**

Joint Fire Science Program (JFSP) Graduate Innovation Award (GRIN), Grant/Award Number: 14-3-01-16; Cooperative State Research, Education, and Extension Service; US Department of Agriculture, Grant/Award Number: ILLU 875-952

Handling Editor: Anna Sala

**Abstract**

- Shifts in rainfall patterns due to climate change are expected to increase drought stress and mortality in forests. Natural and anthropogenic fire regimes are also changing, highlighting the need to understand the interactive effects of fire and drought on tree ecophysiological response and growth.
- Using rainout shelters, we imposed summer drought on natural and planted populations of *Quercus alba* juveniles located in periodically burned and unburned sites in Shawnee National Forest, IL, USA. A subset of planted juveniles was clipped to simulate topkill. We measured predawn leaf water potential ( $\Psi_{pd}$ ), leaf gas exchange ( $A_{max}$ ,  $g_{max}$ ) and relative growth rate (RGR) across treatments to test two hypotheses: (H1) Fire reduces juvenile drought stress by improving water relations through increased root-to-shoot ratios after topkill, or (H2) fire exacerbates juvenile drought stress by promoting a warmer, drier microclimate or amplifying drought-induced nitrogen (N) limitation.
- Burned stands had higher vapour pressure deficits and 13% lower soil inorganic N availability than unburned stands. Rainout shelters reduced soil moisture (0–45 cm) by 10%–24% relative to ambient conditions. Consistent with H2, small, natural resprouts in burned stands experienced greater drought stress than unburned juveniles, with a 7% decrease in leaf nitrogen content (LNC), a 21%–29% reduction in  $A_{max}$  and  $g_{max}$  and a 41% reduction in RGR under drought. Drought effects on unburned juveniles, in contrast, were limited to a 5% reduction in LNC and a neutral to positive effect on leaf gas exchange and RGR. Large natural juveniles were largely unaffected by drought. Recent resprouts (i.e., clipped, planted juveniles) experienced less drought stress than unclipped juveniles, providing partial support for H1.
- Collectively, these results suggest that resprouting after fire can temporarily improve leaf water relations until root-to-shoot ratios re-equilibrate. In contrast, fire can exacerbate drought-driven declines in the growth of small juveniles by both promoting a warmer, drier microclimate and intensifying N limitation. Our results suggest that despite the high drought tolerance of *Quercus* spp., fire-driven changes to local microclimate and resource conditions could limit tree recruitment under future scenarios of rainfall variability.

**KEYWORDS**

drought, fire, microclimate, nitrogen, ontogeny, *Quercus alba*, resprouting, temperate deciduous forest

**1 | INTRODUCTION**

Increased temperatures and more frequent droughts due to climate change are expected to increase drought stress and fire activity in forests (Moritz et al., 2012). In many regions, shifts in moisture and fire regimes may impede tree recruitment with potential large-scale changes to tree species distribution, forest structure and function (Anderegg et al., 2015). Forecasting the response of forests to climate change and developing adaptation strategies require an understanding of the ecological mechanisms governing the vulnerability of juvenile trees to both drought and fire (Enright, Fontaine, Bowman, Bradstock, & Williams, 2015). However, fire–drought interactions are rarely considered, especially with regard to their effects on forest regeneration (Jacobsen & Pratt, 2018; but see Pausas et al., 2015).

Fire disturbance may have opposing effects on the drought vulnerability of juvenile trees because of its impact on multiple ecological processes. For fire-tolerant tree species that survive to resprout, fire exposure directly impacts tree physiology by killing shoot tissue and thus increasing root-to-shoot ratios (Kruger & Reich, 1993; Schwilk, Brown, Lackey, & Willms, 2016). This positively affects tree water relations by reducing losses to transpiration (Kruger & Reich, 1993), although the duration of this effect is unknown. Alternatively, postfire resprouting may result in increased drought vulnerability due to additional effects on juvenile physiology, including carbohydrate depletion (McDowell et al., 2008) or changes in hydraulic function (Jacobsen, Tobin, Toschi, Percolla, & Pratt, 2016). Fire may also indirectly impact juvenile tree physiology through its effects on the environment. The consumption of standing vegetation and leaf litter by fire increases understorey light availability, soil surface temperatures and local evaporative demand, promoting a more xeric microclimate at the soil surface (Nowacki & Abrams, 2008). For young trees still dependent on shallow soil moisture, the environmental effects of fire may intensify drought stress.

Increased fire activity may also intensify drought impacts on forest regeneration by altering nutrient cycling. Drought alone can increase nitrogen (N) constraints on tree growth by limiting decomposition and mineralization rates (Borken & Matzner, 2009; Greaver et al. 2016) as well as N mobility (Gessler et al., 2005) in the upper soil layers where nutrient concentrations are often highest (Jobbágy & Jackson, 2001). Repeated burning can further constrain N availability to juvenile trees through reductions in organic inputs to soil and the loss of surface soil N by combustion (Raison, 1979; Reich, Peterson, Wedin, & Wrage, 2001). Furthermore, fire-driven losses may scale with the N content of fuels, resulting in proportionally greater N losses in ecosystems with high

leaf litter N, such as deciduous forests (Wan, Hui, & Luo, 2001). Consequently, frequent burning and drought may result in N supply being a greater limit on juvenile tree growth than soil moisture. The effects of fire–drought interactions on nutrient cycling may be especially important for drought-tolerant species (e.g., *Quercus* spp.), whose productivity is less commonly constrained by severe water deficit (Brzostek et al., 2014; Klos, Wang, Bauerle, & Rieck, 2009).

Depending on whether resprouting or environmental effects predominate, the impacts of increased burning on forest regeneration could be positive, negative or neutral. Due to the inherent coupling of these direct and indirect effects of fire, however, it has been challenging to identify the prevailing mechanism by which fire alters juvenile tree drought performance. This challenge underscores the need for manipulative field experiments to identify important ecological mechanisms in order to improve model estimates of postfire tree establishment under changing drought regimes (Harvey, Donato, & Turner, 2016). Given juvenile tree establishment is a demographic bottleneck (Grubb, 1977; Ibanez, Clark, LaDeau, & Lambers, 2007) and the life stage often least capable of avoiding drought stress because of restricted root systems (Lyr & Hoffman, 1967), evaluating the competing effects of fire on young tree drought response is critical for understanding and anticipating how recruitment dynamics may change with climate change.

We investigated the effects of fire on tree drought response using a manipulative field experiment on natural and planted juvenile trees. Our main objective was to examine the resprouting and environmental effects of fire on tree drought vulnerability to improve our mechanistic understanding of tree recruitment under climate change. To accomplish our objective, we imposed a realistic drought on juvenile populations located in fire-managed and suppressed areas across multiple stands, quantifying drought vulnerability by measuring tree physiological and growth responses. Juveniles were either natural resprouts or planted individuals clipped prior to leaf-out to simulate topkill from fire. Using planted juveniles allowed us to isolate the environmental from the resprouting effects of fire on drought vulnerability, whereas natural resprouts would be influenced by both resprouting and environmental effects. We tested two hypotheses about how fire affects the drought vulnerability of juvenile trees:

- H1** Fire reduces juvenile drought stress by improving water relations through increased root-to-shoot ratios after topkill
- H2** Fire exacerbates juvenile drought stress by promoting a warmer, drier microclimate and/or intensifying N limitation

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

This study was conducted in the eastern portion of the Lesser Shawnee Hills Ecoregion of the Shawnee National Forest (SNF), located in southern Illinois, USA (37°44'N, 88°67'W). The region is characterized by a humid subtropical climate with a mean annual temperature of 15°C and mean annual precipitation of 1250 mm distributed evenly throughout the year. White oak (*Quercus alba*) was chosen as the study species because it is one of the most abundant and widely distributed tree species in eastern North America. Additionally, *Q. alba* is a moderately drought-tolerant species (Niinemets & Valladares, 2006) capable of vigorous resprouting (Powell & Tryon, 1979) and thus is representative of many *Quercus* species (Abrams, 1990).

### 2.2 | Experimental design

We selected two mature, upland forest sites within SNF that contained both burned and unburned stands. Burned stands were approximately 167 and 263 ha each and experienced three to four prescribed fires from 2002 to 2013, with the most recent fire in February 2013. Records from nearby sites found maximum fire temperatures at the soil surface ranging from 75 to 300°C (Wagner & Fraterrigo, 2015). Unburned stands had no visual evidence of recent burns nor any record of fire activity since at least 1980, according to United States Forest Service records. Both sites had similar elevations (170–200 m) and slopes (10%–25%).

Within each site, we established nine plots on south-facing slopes in burned and nearby (<1 km) unburned stands ( $n = 18$  plots total). South-facing slopes were selected because they are characterized by shallow, well-drained soils where rooting depth is restricted by a fragipan (Bazzaz, 1968), providing a natural means to restrict deep-rooting species (e.g. *Quercus*) from reaching the water-table. Each plot contained two subplots (16 m<sup>2</sup> each) that were spaced approximately 4 m apart to minimize environmental differences. Each subplot was randomly assigned to either drought or ambient moisture treatment ( $n = 18$  subplots each, 36 subplots total). Drought subplots were covered with a 16-m<sup>2</sup> rainout shelter, constructed of clear 0.15-mm-thick polyethylene greenhouse fabric (International Greenhouse Company, Danville, IL, USA) and suspended 2 m above the ground (Supporting Information Figure S1). During 2014 and 2015, rainout shelters were in place for the growing season (April–October) and taken down for the winter to allow for unobstructed litterfall. To account for the artefact of a ~10% reduction in light caused by the rainout shelters, ambient subplots were covered with shade cloth made of deer netting (Dalen Products Inc., Knoxville, TN, USA) suspended 2 m above each plot.

In April 2014, we identified and tagged all existing, natural *Q. alba* juveniles (<1.4 m tall) within the centre 4 m<sup>2</sup> of each subplot to avoid edge effects ( $n = 255$ ). Subplots contained at least three natural *Q. alba* juveniles and few nearby *Q. alba* adults to minimize

the presence of adult stump sprouts. In March 2015, we planted 12 *Q. alba* juveniles, spaced approximately 0.75 m apart, within the centre 4 m<sup>2</sup> of each subplot ( $n = 432$ ). Planted juveniles were 1-year-old, bareroot stock originally grown from seed (Hensler Nursery, Hamlet, IN, USA) that were given 4 weeks to establish before rainout shelters were reinstalled. To help separate the effects of postfire environment from postfire resprouting, half of the planted juveniles in each subplot were randomly assigned to be clipped ( $n = 216$ ), and prior to leaf-out in March 2015, clipped juveniles were coppiced approximately 2 cm above the ground to simulate dieback after fire (Kruger & Reich, 1993). Most ( $n = 196$ ) clipped individuals resprouted from dormant buds near the root collar, and subsequent measurements were made on these resprouts. Throughout, 'resprout' refers to both natural juveniles in burned plots only and clipped, planted juveniles in burned and unburned plots. Although we did not conduct pre- and postfire surveys to confirm resprouting of natural individuals, there was visual evidence (i.e., charred stem with basal sprouts) that strongly supports their classification as resprouts. Natural juveniles in unburned plots were not considered resprouts, as we did not find any visual evidence that individuals had recently resprouted from nonfire forms of injury or growth (e.g., stump sprouting).

### 2.3 | Leaf water potential and leaf gas exchange

To investigate drought–fire effects on *Q. alba* leaf water relations, we measured predawn ( $\Psi_{pd}$ ) and midday leaf water potentials ( $\Psi_{md}$ ) of juveniles once between July 16 to August 25, 2015, on a randomly selected subset of plots. We measured  $\Psi_{leaf}$  on freshly clipped stems containing several mature, undamaged leaves that had been wrapped in foil-laminate bags for 15 min to equilibrate stem and leaf  $\Psi$  prior to clipping.  $\Psi_{pd}$  was measured approximately 1–2 hr prior to dawn and  $\Psi_{md}$  measured between 12:00 and 14:00 using a pressure chamber (PMS 1000, Albany, OR, USA).

To quantify drought–fire effects on maximum leaf gas exchange rates, we measured light-saturated photosynthetic rate ( $A_{max}$ ) and leaf stomatal conductance ( $g_{max}$ ) with an infrared gas analyser (LI-COR 6400, Lincoln, NE, USA). Chamber conditions were set to 1,500  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , 400 ppm [CO<sub>2</sub>], and 400 mol/s air flow while temperature and humidity were set and maintained at ambient levels during each measurement (see Supporting Information Appendix S1). Leaf gas exchange was measured once for natural juveniles between July and August 2014 and again for natural and planted juveniles between June and August 2015.

### 2.4 | Juvenile relative growth rate

We measured juvenile basal diameter, height and number of leaves at the beginning and end of each growing season (May 2014–August 2015 for natural juveniles and May 2015–August 2015 for planted juveniles). To estimate the relationship between size measurements and above-ground biomass (AGB), we harvested *Q. alba* juveniles near the study plots, dried and weighed all above-ground components of each individual. For multistemmed individuals, AGB was

calculated separately for each stem and then summed together. Due to potential differences in tree allometry (Mascaro, Litton, Hughes, Uowolo, & Schnitzer, 2011), we fit separate allometric equations for small (initial height  $\leq 25$  cm) and large juveniles (Supporting Information Table S1). Leaf count was excluded when estimating AGB of planted juveniles because leaf-out was incomplete for many planted individuals during the May 2015 census. We calculated the RGR using the equation:  $[\ln(\text{total final biomass}) - \ln(\text{total initial biomass}) / \text{time interval}]$  (Poorter & Lewis, 1986).

## 2.5 | Environmental covariates

To assess the effectiveness of the drought treatment, we determined gravimetric soil moisture content (SWC) ( $105^\circ\text{C}$ ,  $\text{g H}_2\text{O g soil}^{-1}$ ) in all plots from soil samples collected at 15 cm increments to a depth of 45 cm in June and August. Additionally, we collected continuous volumetric SWC data (15 and 30 cm depths) in 2014–2015 at a subset of the plots ( $n = 6$ ) using data loggers (Onset HOBO Micro Station with EC-5 moisture sensors, Bourne, MA, USA).

To estimate changes to the forest microclimate, we estimated understorey light availability, air temperature and vapour pressure deficit (VPD) across plots. Light availability was quantified in June and August 2015 using a line quantum light sensor (LI-COR 191, Lincoln, NE, USA) (see Supporting Information Appendix S1). Air temperature was measured in 2015 using the HOBO Micro Stations with probes installed 20 cm above the ground surface and covered with white plastic cups to deflect sunlight. Maximum daily air temperature data were used to estimate daily vapour pressure deficit (VPD) for the subset of the plots with minimum daily relative humidity (RH) collected from the nearby ( $< 15$  km) Dixon Springs weather station (Illinois Climate Network 2017).

We explored the effects of drought–fire interactions on N dynamics by quantifying soil inorganic N availability and leaf N content (LNC). Specifically, a pair of activated anion and cation resin membranes ( $6.0 \times 2.5$  cm) were installed at 0–6 cm depth in each plot and left in situ for 30 days (July–August 2014). After removal, membranes were processed and analysed for  $\text{NH}_4^+$ -N using the phenolate method, and  $\text{NO}_3^-$  plus  $\text{NO}_2^-$ -N (hereafter referred to as  $\text{NO}_3^-$ ) using a cadmium column reduction on a Lachat QuickChem 8500 (Hach Company, Loveland, Colorado, USA) (see Supporting Information Appendix S1). To determine LNC, we used leaves from natural ( $n = 42$ ) and planted (unclipped only;  $n = 34$ ) individuals harvested for leaf water potential and analysed each for LNC on a mass basis ( $\text{mg N g}^{-1}$ ) using gas chromatography (Costech Elemental Analyzer, Valencia, CA USA).

## 2.6 | Statistical analysis

We used separate linear mixed-effects models to estimate the effects of drought, fire and their interaction on gravimetric SWC, light, soil N availability and juvenile tree LNC. Site and year were included as additional fixed effects, and plot was coded as a random effect. The effects of drought and fire treatments on continuous volumetric SWC, maximum daily air temperature and VPD were estimated by

first averaging the data by day and then running generalized least-squares models with a first-order, autoregressive covariance structure to account for temporal autocorrelation.

We used linear mixed-effects models to quantify the effects of drought, fire and their interaction on the leaf water potential, leaf gas exchange rates and RGR of natural and planted individuals. We included the fixed effects of initial tree basal area (BA), year (natural juveniles only), clipping (planted juveniles only), total understorey plant cover, site and their interactions with drought and fire. Plot was included as a random effect. Total understorey plant cover was included as a covariate to control for differences in juvenile tree density across plots. Drought and clipping were modelled as a binary or continuous (i.e. gravimetric SWC, 0–15 cm depth and initial juvenile tree BA, respectively) predictors depending on which approach produced the best performing model according to AICc. Analyses were conducted using the 'nlme' package (Pinheiro, Bates, & DebRoy, 2017) in R version 3.3.3 (R Core Development Team, 2017).

Because drought intensity varied among plots, we also modelled plot-level differences in leaf gas exchange and RGR between paired drought and ambient subplots as a function of SWC using ANCOVA. For each plot, we subtracted the mean juvenile tree response in the drought subplot from the mean response in the paired ambient subplot (e.g.  $\Delta\text{RGR} = \text{RGR}_{\text{drought}} - \text{RGR}_{\text{ambient}}$ ). The plot-level response was then modelled as a function of drought-induced change in gravimetric soil moisture (0–15 cm depth;  $\Delta\text{SWC} = \text{SWC}_{\text{drought}} - \text{SWC}_{\text{ambient}}$ ). To account for size-based differences in tree drought response, plot-level responses were calculated separately for each size class (small  $\leq 0.40$  cm<sup>2</sup> initial BA < large; natural juveniles only) and clipping treatment (planted juveniles only). Note that in contrast to the size cut-off used for the allometric calculations (small  $\leq 25$  cm initial height), the median initial BA of natural juveniles (small  $\leq 0.40$  cm<sup>2</sup>) was used as the size cut-off for the ANCOVA models and graphing purposes. For all models, collinearity within each model was assessed by calculating the variance inflation factors (VIF) and excluding any terms with VIF  $> 5$ . Initial juvenile tree BA and soil N availability were log-transformed to achieve normality.

## 3 | RESULTS

### 3.1 | Soil moisture

Drought treatment had a significant effect on soil water content, reducing mean gravimetric SWC (0–45 cm) by 9.4% ( $\pm 3\%$  SE) in 2014 and 19.6% ( $\pm 4\%$ ) in 2015 (drought  $\times$  year  $p < 0.001$ ) relative to ambient conditions across both fire treatments. Averaging across years, drought reduced SWC by 24.4% ( $\pm 5\%$ ) in shallow soils ( $\leq 15$  cm) and 9.6% ( $\pm 3\%$ ) in deep soils (20–45 cm) compared to ambient conditions (drought  $\times$  depth:  $p < 0.001$ ; Supporting Information Figure S2). Daily volumetric SWC showed similar patterns during the 2 years, with the drought treatment reducing shallow and deep volumetric SWC by 34.2% ( $\pm 16\%$ ) and 9.7% ( $\pm 2\%$ ), respectively, relative to ambient conditions (drought:  $p < 0.001$ , drought  $\times$  depth:  $p > 0.05$ ; Figure 1a). Drought-induced reductions in SWC were

marginally greater in unburned than burned plots, but only in 2015 (drought  $\times$  fire  $\times$  year:  $p = 0.08$ ).

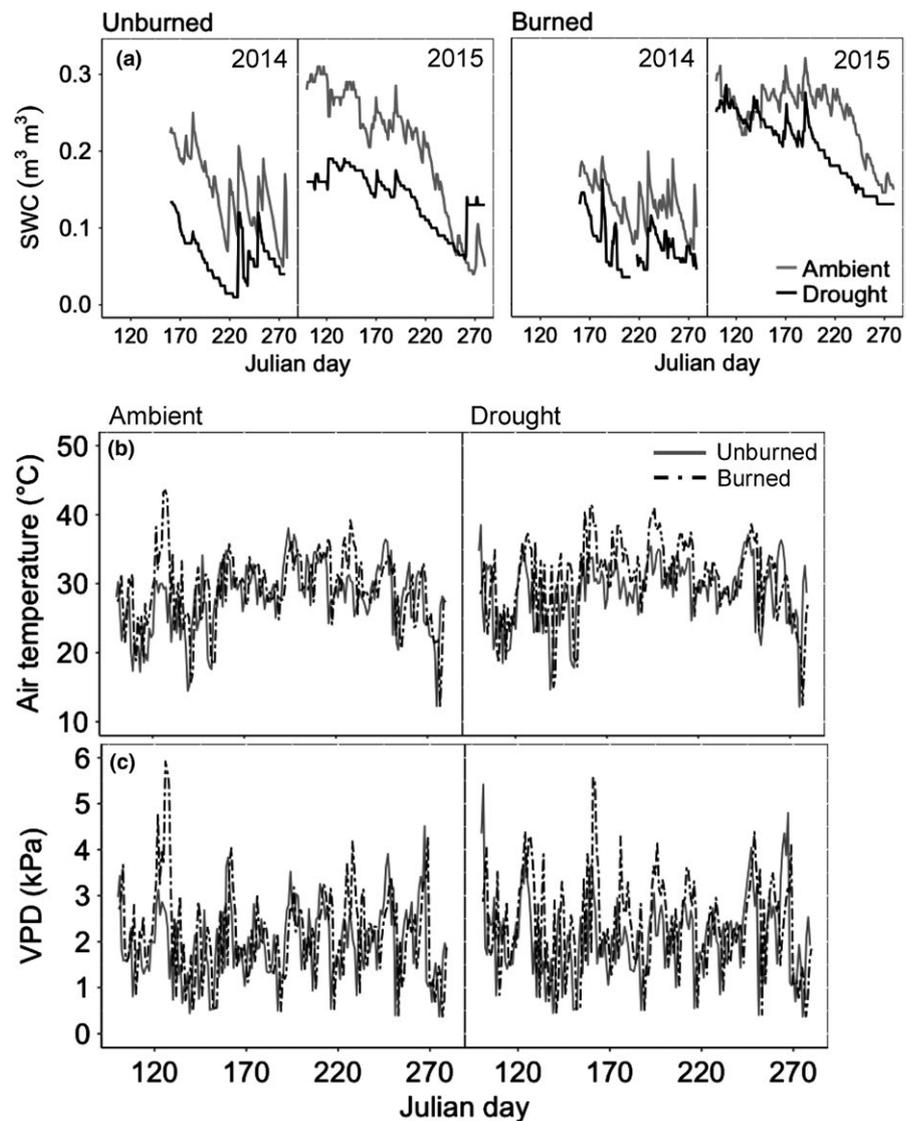
### 3.2 | Microclimate

Burned plots had significantly greater light availability than unburned plots, with understories in burned plots receiving 15.6% ( $\pm 3\%$  SE) of total PAR compared to 6.8% ( $\pm 2\%$ ) in unburned plots ( $p = 0.03$ ). Light availability did not differ between drought and ambient treatments (Supporting Information Figure S3). Maximum daily air temperatures from April to October 2015 were 1.31°C ( $\pm 0.6^\circ\text{C}$ ) higher in burned than unburned plots ( $p < 0.001$ ), and within burn plots, air temperatures were 1.12°C ( $\pm 0.6^\circ\text{C}$ ) higher in drought than ambient subplots ( $p = 0.05$ ) (n.s. drought  $\times$  fire interaction) (Figure 1b). As a result, burned, drought subplots had maximum air temperatures that averaged 2.44°C ( $\pm 1.0^\circ\text{C}$ ) higher than unburned, ambient subplots. Mean daytime VPD was also higher in burned than unburned plots ( $p < 0.001$ ); however, it did not differ with drought treatment and there was no interaction with fire treatment (Figure 1c). Averaging

across drought treatment, mean VPD was 2.03 kPa ( $\pm 0.03$  SE) in unburned plots and 2.24 kPa ( $\pm 0.04$  SE) in burned plots.

### 3.3 | Soil and leaf nitrogen response to drought and fire

Total soil inorganic N availability declined 56.3% ( $\pm 7\%$  SE) with drought ( $p = 0.03$ ; Figure 2) and was 14% ( $\pm 17\%$ ) lower in burned than unburned plots, but only under ambient conditions (drought  $\times$  fire:  $p = 0.04$ ; Figure 2). Small, natural juveniles ( $\leq 0.4$  cm<sup>2</sup> BA) experienced significant declines in LNC ( $-2.73$  mg N g<sup>-1</sup>  $\pm 0.8$ ) with fire treatment (fire  $\times$  sizeclass:  $p = 0.01$ ) and marginal declines ( $-1.19$  mg N g<sup>-1</sup>  $\pm 0.6$ ) with drought (drought  $\times$  sizeclass:  $p = 0.06$ ) (n.s. drought  $\times$  fire interaction) (Supporting Information Figure S4A). LNC of large, natural juveniles did not differ across treatments. Fire and drought significantly reduced the LNC of unclipped, planted individuals by 2.47 ( $\pm 0.7$ ) and 2.33 ( $\pm 0.7$ ) mg N g<sup>-1</sup> relative to unburned and ambient conditions, respectively (fire:  $p = 0.03$ , drought:  $p = 0.04$ , n.s. drought  $\times$  fire interaction) (Supporting Information Figure S4B).

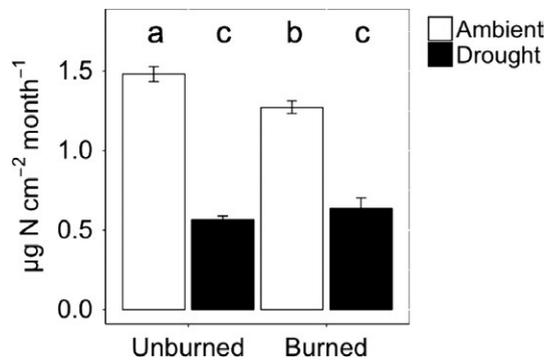


**FIGURE 1** Daily mean (a) volumetric soil moisture content ( $\text{m}^3 \text{m}^{-3}$ ) to 15 cm depth, (b) maximum air temperature ( $^\circ\text{C}$ ) and (c) vapour pressure deficit (VPD, kPa) by fire and drought treatment. Measurements were taken June 9–October 8, 2014, and April 10–October 21, 2015, for SWC and April 10–October 21, 2015, for temperature and VPD

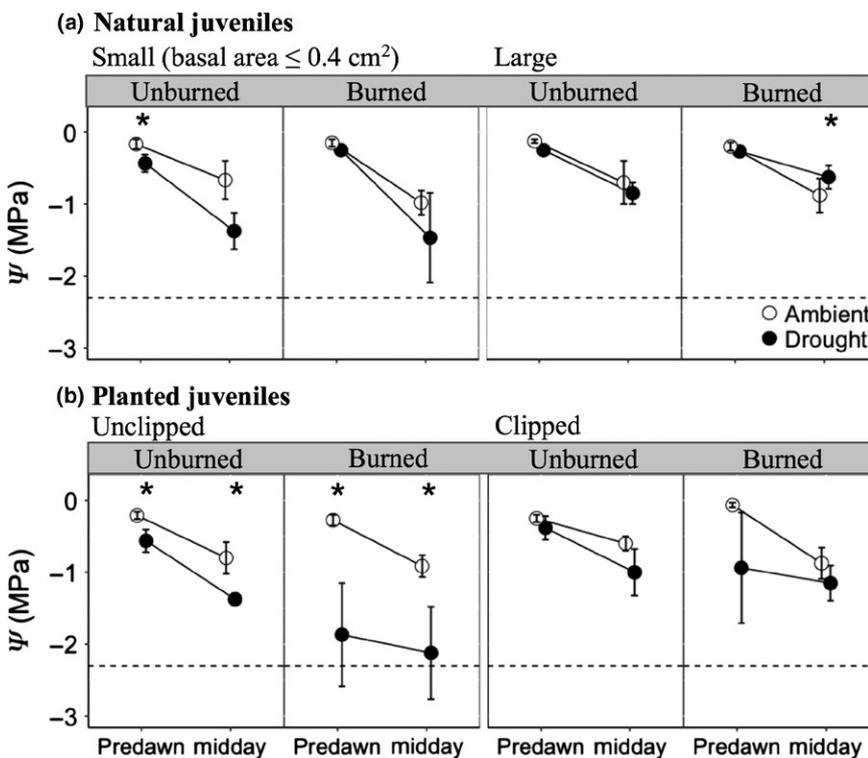
### 3.4 | Leaf water potential response to drought and fire

Drought resulted in small, but significant reductions in predawn ( $\Psi_{pd}$ ) ( $p < 0.01$ ) and midday ( $\Psi_{md}$ ) leaf water potentials of natural juveniles ( $p = 0.02$ ), whereas there was no main or interactive effect of fire on  $\Psi_{leaf}$  (Figure 3a). Drought reduced  $\Psi_{pd}$  of individuals by 0.12 MPa ( $\pm 0.03$  SE) relative to ambient conditions whereas drought effects on  $\Psi_{md}$  depended on tree size: Small juveniles experienced a 0.57 MPa ( $\pm 0.2$ ) reduction while large individuals experienced no change (0.13 MPa  $\pm 0.3$ ) relative to ambient conditions (drought  $\times$  size class:  $p = 0.04$ ).

For planted juveniles, drought effects on  $\Psi_{leaf}$  depended on both fire and clipping treatment (SWC  $\times$  fire  $\times$  clipping:  $p = 0.04$ ).



**FIGURE 2** Mean ( $\pm$  SE) soil inorganic N availability across drought and fire treatments. Values are seasonal means from ion-exchange membranes collected in June and August 2014. Different letters denote significant pairwise differences between treatments ( $p < 0.05$ )



**FIGURE 3** Mean ( $\pm$  SE) predawn and midday leaf water potential ( $M \pm SE$ ) of (a) small (basal area  $\leq 0.4$  cm<sup>2</sup>) and large, natural juveniles and (b) unclipped and clipped, planted juveniles across drought and fire treatments. Values are seasonal means from measurements taken in July and August 2015. Dashed lines indicate the average  $\Psi_{leaf}$  for initiation of stomatal closure in *Q. alba* (Hinckley, Aslin, & Aubuchon, 1978). Significant pairwise differences between ambient and drought treatments are indicated with asterisks ( $*p < 0.05$ )

Specifically,  $\Psi_{pd}$  and  $\Psi_{md}$  for unclipped juveniles were reduced marginally more with drought in burned than unburned plots (unclipped only, SWC  $\times$  fire:  $p = 0.09$ ), whereas  $\Psi_{leaf}$  of clipped individuals was unaffected by drought and fire (Figure 3b).

### 3.5 | Leaf gas exchange response to drought and fire

For natural juveniles, light-saturated assimilation ( $A_{max}$ ) and leaf conductance ( $g_{max}$ ) were reduced more with drought in burned than unburned plots (SWC  $\times$  fire:  $p = 0.07$  and  $p = 0.03$ , respectively; Supporting Information Figure S5), after controlling for tree size, year and understorey cover (Supporting Information Tables S2 and S3). Examining plot-level differences between drought and ambient pairs further revealed that leaf gas exchange rates of small individuals in burned plots declined more steeply with drought intensity than small individuals in unburned plots. Specifically, drought-induced declines in  $A_{max}$  averaged  $-1.94$  ( $\pm 1.1$  SE)  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for small, burned juveniles while being negligible for small, unburned juveniles ( $0.25 \pm 0.7$   $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) (ANCOVA, fire:  $p < 0.01$ ) (Figure 4a). Drought-induced declines in  $g_{max}$  averaged  $-0.03$  ( $\pm 0.02$ )  $\text{mol m}^{-2} \text{s}^{-1}$  for small, burned individuals while small, unburned individuals experienced no effect relative to ambient conditions ( $0.01 \pm 0.02$   $\text{mol m}^{-2} \text{s}^{-1}$ ) (ANCOVA, fire:  $p = 0.03$ ) (Supporting Information Figure S6A). Large juveniles were unaffected by drought regardless of fire treatment.

For unclipped, planted juveniles,  $A_{max}$  and  $g_{max}$  were reduced more with drought for individuals planted in burned than unburned plots (SWC  $\times$  fire:  $p < 0.05$ ) (Supporting Information Tables S4 and S5, Figure S7). Clipping diminished the interactive effects of drought and fire on  $A_{max}$  (SWC  $\times$  fire  $\times$  BA:  $p = 0.06$ ) and  $g_{max}$  (SWC  $\times$  fire  $\times$  BA:  $p = 0.08$ ) such that leaf gas exchange

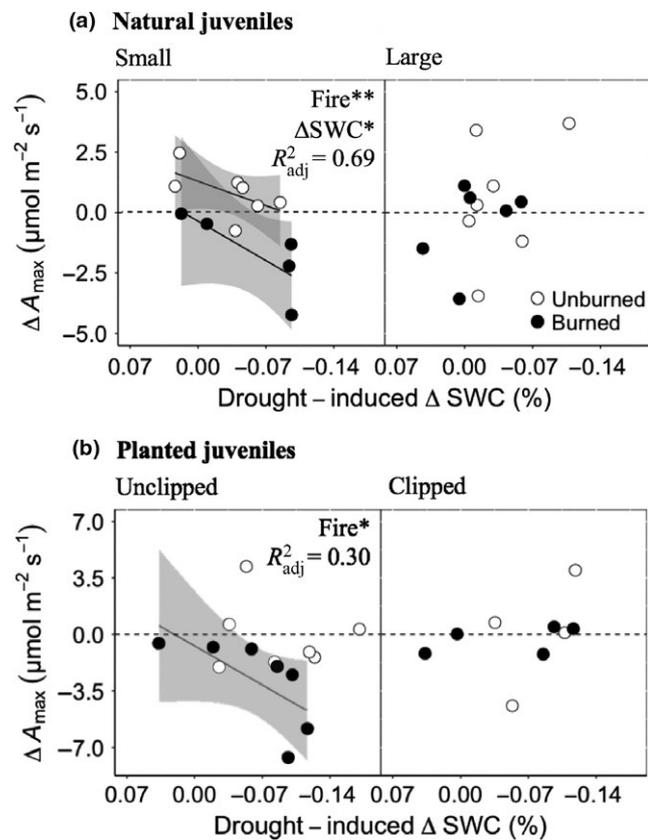
rates of clipped juveniles were unresponsive to drought and fire (Supporting Information Tables S4 and S5, Figure S7). Examining plot-level differences revealed that leaf gas exchange rates of unclipped juveniles planted in burned plots declined more steeply with drought intensity than those planted in unburned stands. Specifically, drought-induced declines in  $A_{\max}$  averaged  $-2.73$  ( $\pm 1.2$  SE) and  $-0.16$  ( $\pm 0.9$ )  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for those planted in burned and unburned plots, respectively (ANCOVA, fire:  $p = 0.03$ ) (Figure 4b). Drought-induced declines in  $g_{\max}$  averaged  $-0.04$  ( $\pm 0.02$ )  $\text{mol m}^{-2} \text{s}^{-1}$  for unclipped juveniles planted in burned plots while being negligible for juveniles planted in unburned plots (ANCOVA, fire:  $p < 0.01$ ) (Supporting Information Figure S6B).

### 3.6 | Relative growth rate response to drought and fire

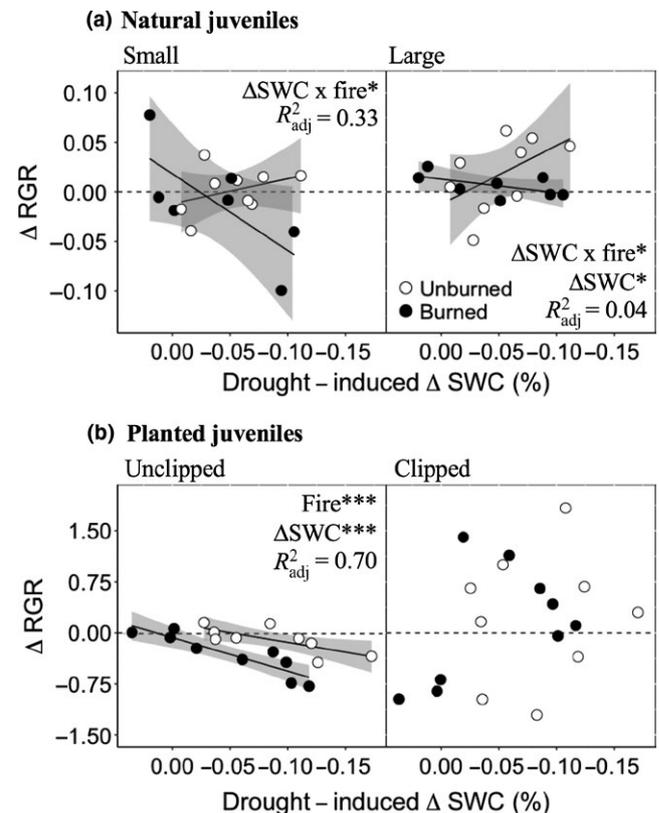
The effect of drought on the relative growth rates (RGR) of natural juveniles depended on fire (SWC  $\times$  fire:  $p = 0.02$ ), with unburned individuals showing a positive response and burned individuals

showing a negative response to drought relative to ambient conditions, after controlling for tree size and site (Supporting Information Table S6). Plot-level comparisons revealed that the effects of drought on RGR depended on drought intensity, fire treatment and tree size (Figure 5a). Fire significantly affected the direction of juvenile growth response to drought; the RGR of burned juveniles decreased with increasing drought severity whereas the RGR of unburned juveniles increased (SWC  $\times$  fire:  $p = 0.03$ ) (Figure 5a). In burned plots, the RGR of small juveniles was reduced marginally more by drought than large juveniles (for burned plots only, SWC  $\times$  size class:  $p = 0.07$ ) (Supporting Information Figure S8). There was not a significant three-way interaction between drought, fire and tree size.

For planted juveniles, drought reduced RGR for unclipped but not clipped individuals relative to ambient conditions (SWC  $\times$  clipping:  $p < 0.001$ ; Supporting Information Figure S9), after controlling for initial tree size (Supporting Information Table S7). Plot-level comparisons show that the RGR of unclipped juveniles was reduced significantly more by drought in burned than unburned plots (for unclipped only, fire:  $p < 0.001$ ), whereas fire had no effect on clipped juveniles (Figure 5b).



**FIGURE 4** Drought-induced change (drought – ambient) in plot-level mean light-saturated assimilation ( $\Delta A_{\max}$ ) of (a) small (basal area  $\leq 0.4$  cm<sup>2</sup>) and large, natural *Q. alba* juveniles and (b) unclipped and clipped, planted *Q. alba* juveniles as a function of drought-induced change in gravimetric soil water content ( $\Delta\text{SWC}$ ; 0–15 cm). Values are interannual means (June to August 2014 and 2015) for natural juveniles and seasonal means (June to August 2015) for planted individuals. Black lines represent significant regressions with 95% CI



**FIGURE 5** Drought-induced change (drought – ambient) in plot-level mean relative growth rate ( $\Delta\text{RGR}$ ) of (a) small (basal area  $\leq 0.4$  cm<sup>2</sup>) and large, natural *Q. alba* juveniles and (b) unclipped and clipped, planted *Q. alba* juveniles as a function of drought-induced change in gravimetric soil water content ( $\Delta\text{SWC}$ ; 0–15 cm). Growth was observed from May 2014 to August 2015 for natural juveniles and from May 2015 to August 2015 for planted individuals. Black lines represent significant regressions with 95% CI

## 4 | DISCUSSION

We used a field experiment to investigate how fire affects juvenile tree drought performance. Comparing the responses of natural *Q. alba* juveniles with those of planted individuals allowed us to differentiate between potential positive, resprouting effects (H1) and negative, environmental effects (H2) of fire on drought response. In partial support of H1, we found clipped, planted individuals that recently resprouted maintained higher leaf water potentials (Figure 3b), assimilation rates (Figure 4b) and RGR (Figure 5b) during drought than unclipped, planted individuals. In support of H2, we observed appreciable drought-driven declines in LNC (Supporting Information Figure S4), leaf gas exchange (Figure 4) and above-ground RGR (Figure 5) for small natural resprouts and unclipped planted juveniles in burned plots, suggesting the warmer and drier conditions as well as reduced N availability observed in burned stands exacerbates drought stress for small juveniles. Together, these results indicate that fire-driven changes to forest microclimate and N cycling overwhelm the shorter-term benefits of resprouting on drought vulnerability. Ultimately, however, we find the susceptibility of *Q. alba* juveniles to these drought–fire interactions declines with ontogeny, presumably due to the development of a deep root system. To our knowledge, this is the first field experiment to separate the direct, resprouting effects from the indirect, environmental effects of fire disturbance on juvenile tree drought vulnerability. These findings indicate that fire can interact with drought through multiple ecological mechanisms to influence the growth of juvenile trees and consequently, drought–fire interactions are important to consider when forecasting future forest regeneration under climate change.

### 4.1 | H1: Burned resprouts will have improved water relations and drought performance relative to unburned controls

We found limited support that resprouts have improved water relations relative to unburned, nonresprouting individuals. Specifically, clipping of planted individuals resulted in smaller reductions in leaf water potential with drought relative to unclipped controls (Figure 3b). In contrast, the water relations of natural juveniles were largely unaffected by our experimentally imposed drought, regardless of whether they were resprouts (Figure 3a). The lack of drought effects on the predawn leaf water potential of natural juveniles suggests that these individuals were capable of accessing deeper soil moisture. Despite this, leaf gas exchange rates and RGR of small, natural juveniles were reduced more by drought in burned than unburned plots, in contrast with the response of clipped planted juveniles, which did not differ with fire treatment (Figures 4 and 5). Taken together, these results suggest that the benefits of resprouting for overall drought performance are temporary and can be overwhelmed by the environmental effects of fire.

Our findings are consistent with past studies that find resprouts maintain better water status under drought than nonresprouting

individuals, but only for the first few years after fire (Clemente, Rego, & Correia, 2005; Fleck, Hogan, Llorens, Abadía, & Aranda, 1998; Pena-Rojas, Aranda, & Fleck, 2004). Resprouts rapidly reallocate biomass above-ground after fire (Del Tredici, 2001) and as a result can quickly regain leaf area and transpiration rates. Of the few studies that examined the long-term influence of resprouting on drought response, they found the effects on juvenile tree ecophysiology were limited to 4–5 years (Hodgkinson, 1992; Wellington, 1984). Results from our study suggest the effects of resprouting on *Q. alba* water relations are limited to <3 years. While planted individuals were clipped immediately prior to the study, postfire resprouting of natural juveniles occurred 3 years prior to the beginning of the experiment (March 2013). Although we did not measure root-to-shoot ratios, natural resprouts had more time than clipped, planted juveniles to return to prefire root-to-shoot ratios.

The physiological and growth responses of large, natural resprouts and clipped, planted individuals were similarly or less affected by drought than their nonresprouting counterparts (e.g., Figures 3 and 5). Our finding contrasts with other work suggesting that resprouts may be more susceptible to drought stress and mortality than unburned individuals due to carbohydrate depletion (McDowell et al., 2008; Pausas et al., 2015; Pratt et al., 2014) or changes in hydraulic structure and function, for example, increased cavitation risk (Jacobsen et al., 2016). Although we did not measure carbohydrates or cavitation risk, there are at least three key differences between our study and those that find negative effects of resprouting on drought vulnerability: fire season, fire frequency and drought severity. First, both fire-induced resprouting and clipping occurred prior to leaf-out in our study, which likely minimized the depletion of below-ground reserves (starch and nutrients) relative to studies of resprouts recovering from summer fires when carbohydrate reserves are at seasonal lows (Pratt et al., 2014). Second, our study concerned periodic fire disturbance (3–4 year return interval) rather than the more frequent disturbances (<2 year interval) shown to exhaust tree carbon reserves (Bonfil, Cortes, Espelta, & Retana, 2004). Finally, as indicated by the relatively small declines in leaf water potential (Figure 3), our experimental drought was less severe than natural and experimental droughts documented in other studies (McDowell et al., 2008; Pratt et al., 2014). Regardless of disturbance timing or frequency, resprouts will not deplete their carbohydrate stores if the drought event is too short or low intensity to impose stomatal restriction (McDowell et al., 2008).

### 4.2 | H2: Effects of burning on the environment will exacerbate drought effects

We found that within 15 years of reintroducing prescribed fires, burned forest understories had higher maximum air temperatures and VPD than unburned forests (Figure 1). These fire-driven changes in microclimate had significant functional consequences for both small, natural juveniles and unclipped, planted *Q. alba* juveniles, which showed greater drought-induced declines in assimilation and growth in burned than unburned forests, in support of H2 (Figures 4

and 5). Our results are consistent with past research that finds under shade conditions where sunlight is the primary limitation for plant growth, water stress often has minimal impacts on plant performance (i.e. the light–water model; (Canham et al., 1996; Holmgren, Scheffer, & Huston, 1997). With the reintroduction of fire and opening of the forest canopy, plant growth becomes less light-inhibited and instead, more responsive to soil moisture and other limiting resources (Wagner & Fraterrigo, 2015).

Our findings are novel in that they suggest recurrent surface fires can have lasting effects on forest understorey microclimate which in turn have negative consequences for juvenile trees exposed to drought. Most studies concerning the functional consequences of fire-driven changes to environmental conditions have focused on stand-replacing crown fires. Unlike surface fires, crown fires often reduce canopy leaf area and tree density, resulting in increased throughfall and reduced evapotranspiration (Cardenas & Kanarek, 2014; Silva, Rego, & Mazzoleni, 2006) as well as reduced air temperature via increased air movement through the understorey (Chen, Franklin, & Spies, 1995). As a result, trees regenerating from crown fires can exhibit higher water availability than unburned individuals (Clemente et al., 2005; Parra & Moreno, 2017). In contrast, repeat surface fires can increase solar radiation and temperatures in the understorey (Hart, DeLuca, Newman, MacKenzie, & Boyle, 2005; Iverson & Hutchinson, 2002), especially on south-facing slopes, where solar radiation and daily temperatures reach their extremes (Chen et al., 1995). Our results show that fire-driven changes to understorey light availability can be particularly important in closed canopy forests, where relative increase in light levels between unburned and burned forests can be substantial (i.e. two-fold increase, Supporting Information Figure S3) (Hart et al., 2005; Iverson & Hutchinson, 2002). Furthermore, unlike evergreen woody species adapted to drought-prone environments that experience crown fires (i.e. chaparral shrublands), deciduous broadleaf tree species like *Q. alba* are relatively shade tolerant and thus characterized by lower leaf mass per area and relatively higher water and nitrogen demand (Valladares & Niinemets, 2008). Such traits may predispose them to even moderate changes to microclimate and other fire-driven impacts (e.g. N limitation) more than highly drought-adapted, sclerophyllous vegetation (Quero, Villar, Marañón, & Zamora, 2006). Our findings suggest that these moderate changes to forest microclimate can have strong, persistent effects on the drought vulnerability of small juveniles and underscores the importance of studying drought–fire interactions in both xeric and mesic environments.

### 4.3 | Drought–fire interactions on N cycling

In addition to microclimate effects, we found that the dual disturbances of fire and drought had negative, nonadditive effects on soil N availability and LNC of small juveniles (Figure 2 and Supporting Information Figure S4). Our results from ambient, burned plots are consistent with a recent meta-analysis that projected that long-term, fire-driven N losses will suppress the productivity of temperate broadleaf forests (Pellegrini et al., 2017). However, the observed

reductions in soil N availability with fire were small compared to drought-driven effects. Lack of soil moisture can limit plant nutrient uptake by reducing N mineralization rates (Borken & Matzner, 2009), but also by limiting diffusion and mass flow of nutrients to roots (Kreuzwieser & Gessler, 2010). As a result, tissue N concentrations and photosynthetic capacity can decline (Field & Mooney, 1986; Reich, Walters, & Ellsworth, 1991). Indeed, we found a weak, positive correlation between juvenile LNC and assimilation rates (Supporting Information Figure S10). Although water stress frequently limits photosynthesis and growth, most studies identify stomatal closure rather than N limitation as the primary mechanism by which water stress reduces plant carbon gain (Bota, Medrano, & Flexas, 2004; Kuster, Schleppei, Hu, Schulin, & Günthardt-Goerg, 2012). Our findings suggest that under conditions of prolonged but less severe moisture stress, drought-driven reductions in nutrient supply may be a more important constraint on oak regeneration dynamics than water limitation. Further studies are needed on the relative importance of drought effects on N uptake relative to CO<sub>2</sub> assimilation in less drought-prone ecosystems (e.g. temperate broadleaf forests).

### 4.4 | Response to drought–fire interactions shifts with tree ontogeny

Our results show that the vulnerability of juvenile trees to drought–fire effects varies with ontogeny, likely due to changing tolerances and strategies for coping with stress as trees mature (Fisichelli et al., 2014; Niinemets, 2010). Although we did not quantify the below-ground biomass of juveniles, root biomass and rooting depth generally scale positively with above-ground size in trees (Cairns, Brown, Helmer, & Baumgardner, 1997; Dawson & Ehleringer, 1991; Mokany, Raison, & Prokushkin, 2006). As soil moisture became depleted in upper soil layers (Supporting Information Figure S2), larger juveniles with greater access to deep soil water (Dawson, 1996; Lyford, 1980) were better equipped to avoid water and nitrogen stress during drought, especially in burned environments.

Specifically, our findings suggest a size threshold (0.4 cm<sup>2</sup> BA) below which *Q. alba* juveniles are most vulnerable to the environmental-mediated effects of fire on drought stress. Similarly, Cavender-Bares and Bazzaz (2000) found that drought vulnerability of *Q. rubra* was highest for individuals smaller than ≈ 0.8 cm<sup>2</sup> BA. Our study identifies a specific ontogenetic threshold that may help to improve predictions of regeneration dynamics under changing drought and fire regimes. Additionally, these results underscore the need for additional, mechanistic research on the response of natural, field-grown juvenile trees to varying drought intensities in order to inform predictions of forest vulnerability to climate change (McDowell, Ryan, Zeppel, & Tissue, 2013).

## 5 | CONCLUSIONS

By studying the functional response of natural and planted populations of a resprouting tree species to an experimental drought

imposed in sites with contrasting fire histories, we were able to evaluate the relative ecological importance of postfire resprouting vs. environmental conditions on juvenile tree water relations and growth during drought. We discovered that both planted and small, natural *Q. alba* juveniles in repeatedly burned forests experienced significantly greater drought-induced declines in leaf gas exchange and growth rates than individuals in unburned forests, most likely due to fire-driven changes to microclimate. We show that the positive effects of postfire resprouting on drought avoidance are temporary and outweighed by the effects of environmental changes resulting from fire. Our results suggest that despite the high drought tolerance of *Quercus* spp., changes to the forest microclimate from periodic surface fires can significantly reduce the drought resistance of small, *Q. alba* juveniles that have yet to develop deep tap roots. To understand postfire regeneration under drought, more studies are needed that span a wider range of fire and drought regimes. As our findings highlight, even low-intensity surface fires may have unanticipated negative consequences for forest recruitment in a changing climate.

## ACKNOWLEDGEMENTS

Authors would like to thank Evan DeLucia and David Rosenthal for providing equipment and Martha Langill, Valarie Repp and Jennifer Woodyard for field and laboratory assistance. This study was supported by a Joint Fire Science Program (JFSP) Graduate Innovation Award (GRIN) Project ID 14-3-01-16 and by the Cooperative State Research, Education, and Extension Service, US Department of Agriculture, under project number ILLU 875-952.

## AUTHORS' CONTRIBUTIONS

T.R. designed the research, collected and analysed the data. T.R. led the writing of the manuscript and J.F. contributed substantially to data interpretation and revisions. All authors gave final approval for publication.

## DATA ACCESSIBILITY

Data used in this article are available in Dryad Digital Repository: <https://doi.org/10.5061/dryad.56t8j52> (Refsland & Fraterrigo, 2018).

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## SUPPORTING INFORMATION

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

**How to cite this article:** Refsland T, Fraterrigo J. Fire increases drought vulnerability of *Quercus alba* juveniles by altering forest microclimate and nitrogen availability. *Funct Ecol*. 2018;00:1–12. <https://doi.org/10.1111/1365-2435.13193>