Forest Science
https://doi.org/10.1007/s44391-025-00022-y

ORIGINAL ARTICLE

Regeneration Response to Shelterwood-Burn Treatments in a Dry Oak-Dominated Forest

Sarah J. Rademacher[1,2] · Daniel C. Dey[3] · John M. Kabrick[3] · Robert W. E. Quackenbush[1,4] · Michael R. Saunders[1] · J. Travis Swaim[5] · Christopher D. Thornton[5] · Michael A. Jenkins[1]

Received: 14 June 2024 / Accepted: 18 February 2025

Abstract

Alterations to the fire regime have contributed to widespread regeneration failure in oak (*Quercus*) forests of the eastern United States. Our long-term study was initiated in 2010 in southern Indiana to examine how oak reproduction in a dry oak forest responded to shelterwood and midstory treatments followed by a spring prescribed burn. We tracked the survival, height, and resprout response of individual seedlings through time, and tallied overall seedling density pre- and post-treatments. Mixed-effects models and nonmetric multidimensional scaling (NMDS) ordination were used to evaluate post-treatment response in 2020 and 2021. Following the burn, monitored oak seedlings had greater survival (> 94%) and resprouting (> 92%) than most competing species, including maple species (*Acer* spp. ~ 59% survival and resprouting) and white ash (*Fraxinus americana*; 72% survival and resprouting). White oak (*Q. alba*) doubled in seedling density after burning and was one of the most abundant species (9,864 stems ha^{-1}) in the regeneration stratum. NMDS ordination indicated that the burn promoted a shift away from mesophytic species towards greater importance of oak species. A shelterwood treatment, followed by single prescribed burn, at our study site has likely produced adequate density of oak reproduction to ensure future dominance by the genus, particularly on less-productive south-facing slopes.

Study Implications

Beyond their timber value, oak species are critical to wildlife species and their decline in dominance results in a loss of ecosystem services. Regenerating oak species is time and labor intensive, typically requiring multiple prescribed burns in combination with shelterwood harvests. However, our study conducted on a xeric site found adequate densities of competitive oak seedlings following a single burn conducted after a shelterwood establishment cut. This suggests that management activities on xeric sites could help maintain oak species across forest landscapes

Extended author information available on the last page of the article

Published online: 19 March 2025

with less effort than on mesic sites where repeated burning and other follow up treatments may be required.

Keywords Prescribed fire · Oak reproduction · Seedling survival · Long-term study · Species composition

Introduction

Oaks (*Quercus* spp.) are foundation species in forests throughout the world by contributing to complex stand structure and providing critical mast for multiple wildlife species (Lindbladh and Foster 2010; Hanberry and Nowacki 2016; Rawat et al. 2022). However, the persistence of oak forests in eastern North America is threatened by a multitude of factors including acorn predation, climatic change, damage by insects and deer, and excessive competition resulting from decreased fire frequency, all of which have contributed to a lack of competitive reproduction (Lorimer 1993). Prior to European settlement, Native Americans used periodic fires to favor desired plant and animal species and clear land for farming (Parker and Ruffner 2004; Jenkins 2013). This fire regime resulted in more open forests (Hanberry et al. 2014), and favored the accumulation of large densities of competitive advance reproduction of oak species (Johnson et al. 2019). Historic fire return intervals varied, and occasional longer fire-free periods allowed oak reproduction to grow large enough to withstand damage and/or mortality during subsequent burns (Dey 2014).

Decades of fire suppression contributed to the development of densely shaded and overstocked forests, driving the process of "mesophication", a compositional shift from xerophytic and pyrophilic species, including oaks, toward dominance by mesophytic species, such as maples (*Acer* spp.; Nowacki and Abrams 2008). This shift towards mesophytic species dominance has been well documented in eastern forests (Abrams and Downs 1990; Jenkins and Parker 1998; Palus et al. 2018), with mesic sites typically changing more rapidly than xeric sites (Abrams 1992; Olson et al. 2014, but see Palus et al. 2018). Forest conditions become unfavorable to fire as shade and humidity increase, and mesophytic litter is less flammable than oak litter (Varner et al. 2016).

Research has shown mixed success in establishing oak reproduction using prescribed fire in the absence of overstory manipulation; however, combinations of prescribed fire and silvicultural techniques to reduce overstory and midstory density have been implemented with positive results depending on site conditions (Brose et al. 2014; Vander Yacht et al. 2019). For example, Brose et al. (1999a) recommended an establishment cut to increase light and stimulate root growth of existing oak seedlings, germinate seeds of competing species, and allow the remaining canopy trees to provide enough leaf litter to facilitate desired prescribed fire effects. Under these conditions, the establishment cut provided a favorable environment for oak regeneration by increasing light on the forest floor, while also providing partial shade and protection from extreme temperatures and wind, and suppressing regeneration of aggressive shade-intolerant species such as tuliptree (*Liriodendron tulipifera*; Dey 2014). After the establishment cut, a 3-to-5-year period precedes prescribed fire and allows oak reproduction to respond to the release. Fire is then applied and repeated as needed. While the shelterwood-burn method was developed on more productive (mesic) sites (white oak $SI_{50} = 21–24$ m; Brose et al. 1999a), additional studies are needed to determine how the technique is best applied to less productive (xeric) sites (white oak $SI_{50} < 21$ m).

Midstory treatments implemented before or after overstory harvests may favor oak regeneration by further increasing light and reducing competition. According to Schlesinger et al. (1993), overstory harvest without understory/midstory treatments may be adequate to favor oak regeneration on less productive sites but midstory treatment may be needed on more productive sites. Midstory treatments in oak forests have been shown to increase growth of oak seedlings compared to sites without treatment (Craig et al. 2014). The application of midstory treatments in conjunction with overstory removal may improve oak seedling growth (Loftis 1990), but also favors the growth of competitors (Hackworth et al. 2020).

Research has highlighted the benefits of repeated burning, including the promotion of acorn germination and the establishment of seedlings under conditions of reduced litter depth, reduced interspecific competition, and increased light availability (Brose et al. 2013; Dey 2014). Meta-analyses have shown mostly neutral to positive effects of repeated burning on oak regeneration, depending on harvest history, site productivity, or season of burn (Brose et al. 2013). Two burns following a thinning in southern Ohio yielded increased oak densities on intermediate and xeric sites, while mesic sites continued to have lower densities, particularly in larger size classes (> 50 cm height; Iverson et al. 2008).

A large proportion of research examining oak regeneration has focused on the use of multiple fires to establish oak on more productive sites. However, the prevalence of xeric oak forests in the eastern United States warrants studies to determine if fewer burns can be applied to influence oak regeneration on less productive sites that typically have lower pH and nutrient availability, conditions associated with greater importance of oak species (Swaim et al. 2018). With a slower rate of mesophication on drier sites, oak reproduction may be advanced with fewer burns, requiring less effort and cost by land managers. When combined with silvicultural treatments, a single fire on these less productive sites could promote adequate oak regeneration to ensure dominance in the developing stand.

In this study, we investigated whether one prescribed burn produced adequate oak regeneration after an establishment cut in a xeric oak-dominated forest with and without midstory treatments. We evaluated oak seedling survival, resprouting, growth, abundance, and competitiveness compared to competing species to address the following questions:

(1) Does a shelterwood harvest followed by a single prescribed burn on a xeric site lead to successful oak regeneration without the need for repeated burns? We predicted that oak seedlings would have higher survival, growth, and abundance

compared to mesophytic species, due to oak's ability to survive fire, resprout, and compete on dry sites. We further predicted that post-burn stand and edaphic variables associated with lower site productivity will be associated with a compositional shift towards greater dominance of oaks species.

(2) How does the response of the regeneration layer differ with midstory treatments (mechanical, herbicide, vs. none)? We predicted that seedlings would display greater growth and abundance in the chemical/mechanical treatments versus no midstory removal due to increased light reaching the regeneration layer.

Methods

Study Site

We collected data on the Hoosier National Forest (HNF), which is located across nine counties of southern Indiana within the Crawford Upland Section of Indiana (Homoya et al. 1985; Van Kley et al. 1995). Oak-hickory (*Quercus-Carya*) is the dominant forest type within the Section, with beech-maple (*Fagus-Acer*) forest also occurring on mesic sites (Homoya et al. 1985). Records indicate that 69% of the stands in the HNF were established between 1800 and 1940 (Parker and Ruffner 2004). The soils are mainly sandstone derived, with a few shale or limestone outcrops, and are largely silt loams or fine sandy loams and occasionally silty clay loams (Van Kley et al. 1995). Soils of the study area were mapped as the Ebal-Deuchars-Kitterman complex, 12–24% slopes (Oxyaquic and Aquic Hapludalfs), Apalona-Zanesville silt loams, 6–12% slopes (Oxyaquic Fragiudalfs), and the Adyeville-Tipsaw-Ebal complex, 20–50% slopes (Typic Hapludalfs and Dystrudepts, and Oxyaquic Hapludalfs; Soil Survey Staff 2023).

Our study site is located approximately 35 km northeast of Tell City, Indiana (Fig. 1), approximately 5 km north of the Ohio River. The site is dominated by white oak (*Q. alba*) and post oak (*Q. stellata*) on dry slopes with American beech (*F. grandifolia*) and sugar maple (*A. saccharum*) on mesic slopes and ridges. The study area has an average SI_{50} of 17.6 m for white oak and consists of eight units subjected to different combinations of silvicultural treatments. Prior to our study, no fires were recorded within the study area.

Overstory and Midstory Treatments

Our study site received a shelterwood establishment cut across eight units ranging in size from 2.2 to 8.1 ha with a total treatment area of 28.9 ha. The shelterwood treatment generally followed the shelterwood-burn method described by Brose et al. (1999a) with an establishment cut that removed competing species, such as sugar maple, tuliptree, and American beech, and poor-quality trees (DBH ranging from 11.4 to 63.0 cm), while leaving dominant and codominant oak and hickory trees. Across units, basal area was reduced from an average of 25.3 to 11.0 m^2 ha^{-1}. All harvests were conducted between May 2012 and October 2015.

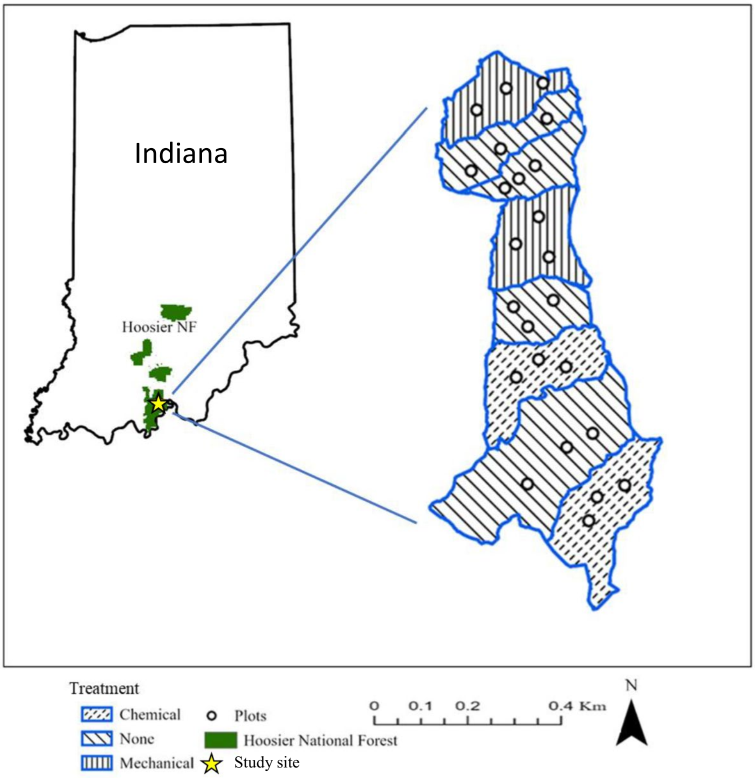

Fig. 1 Study site located within the Hoosier National Forest of southern Indiana (star). Chemical = shelterwood with chemical midstory removal, none = shelterwood without midstory removal, mechanical = shelterwood with mechanical midstory removal

Four units received a non-commercial midstory treatment in spring of 2015 (Turman Creek Tree Farms 2013; Table S1). Two units received a mechanical treatment in which all non-merchantable stems > 2.54 cm DBH were cut with chainsaws without herbicide treatment and the other two units received herbicide treatment of stems > 2.54 cm and up to 17.8 cm DBH. Cut stump or girdled trees were treated with Pathway herbicide (10.2% picloram + 39.6% 2,4-D) or a comparable mixture diluted to 50%. The other four units did not receive midstory treatment.

Prescribed Burn

The USDA Forest Service (Forest Service) conducted a dormant season burn using aerial ignition and drip torches on April 16, 2019. The fire was applied 4–7 years after the original harvests and burned a total of 301 ha, including the study site. Air temperatures ranged between 23.3–29.4 ^{O}C, relative humidity between 28–35%, and winds between 3–11 km hr^{-1} with gusts up to 14 km hr^{-1} during the fire. Flame lengths ranged from 25–36 cm, heights from 13–20 cm, and rate of spread from

10–40 m hr^{-1} with a head fire flame height of 61–91 cm and length of 1.2 m (Harriss 2019).

Plot Design and Field Measurements

In 2010, three permanent plots were established in each unit across all treatments for a total of 24 plots. Each unit was stratified based upon topography and plot locations were randomly assigned within delineated topographic positions at least one tree height from stand borders to avoid edge effects. Each plot consisted of a 0.047 ha overstory plot (12.6 m radius), a 0.016 ha concentric midstory subplot (8.0 m radius), a 40.5 m^2 regeneration subplot (3.6 m radius; 6 m from plot center at 45° azimuth), twelve 1-m^2 circular vegetation quadrats (at 3, 6, 9, and 12 m along 12 m transects oriented at 135, 225, and 315^0 azimuths from plot center), and four fuel transects (12.6 m in length; oriented from plot center at 0, 90, 180, and 270^0 azimuth). Pretreatment data were collected for the overstory and regeneration layer in 2010. Site data (percent slope, aspect, and terrain shape index [TSI; McNab 1989]) were also measured. Data were also collected during and after treatments in 2012, 2013, 2014, 2015, and 2018.

Fire Monitoring

We measured fire temperatures during the April 2019 burn and char heights directly after to quantify fire intensity and severity. We placed stakes with aluminum paint tags 12.6 m from the main plot center in cardinal directions and one at the plot center with two paint tags on each stake; one tag approximately 30.5 cm above the ground and the other at the litter surface. Six dots of heat-activated Tempilaq® paint with activation temperatures of 79.4, 121.1, 162.8, 204.4, 315.6, and 426.7 ^{0}C were applied to each tag. Tags melt at 661.1 ^{0}C. After the burn, tags were evaluated for temperature based on the activation of the paint dots. In addition, prior to the burn we buried one HOBO® Temp datalogger approximately 10 cm deep at each plot center with the thermocouple approximately 30.5 cm above the ground to record the temperature every three seconds during the burn. Due to the length of time the HOBO devices were in the ground, many of them did not collect data. However, we had at least one working device from each treatment unit, except unit 8. In 2021 post-burn, char height was measured on trees of varying species and DBH on each overstory plot, ranging from 9 to 21 trees per plot.

Overstory and Midstory Sampling

In the summers of 2010 (pre-treatments) and 2020, we measured the DBH of: (1) tagged live trees and snags $\geq$ 11.4 cm DBH within the 0.047 ha circular plots in each treatment unit and (2) tagged live midstory trees $\geq$ 3.81 cm and $<$ 11.4 cm DBH within a concentric 0.016 ha circular subplot. We tagged, measured DBH, and identified species of all ingrowth trees. We also recorded survival status (alive/dead) of midstory and overstory trees one-year (2020) and two-years post-burn (2021). We used a concave spherical densiometer to estimate canopy closure (Lemmon 1957) within the 40.5 m^2 regeneration subplot.

Tree Reproduction Sampling

In 2010 prior to treatments, an average of 38 (ranging from 19 to 59) seedlings (< 3.81 cm DBH) of varying species and heights were tagged for continued monitoring in each 40.5 m^2 regeneration subplot. In 2020, we reassessed each tagged seedling for survival status (alive, dead, missing), basal diameter (~ 1.27 cm above ground, to nearest 0.03 cm), height (to nearest 0.3 cm), and origin (seed origin, mature stem resprout, or seedling resprout). In addition, we recorded the number of resprouts and the height and basal diameter of the tallest stem. Survival status, height, and basal diameter of the tallest stem, and the number of sprouts were reassessed in the summer of 2021 (two-years post-burn). Within each plot, we also tallied tree reproduction in a 40.5 m^2 subplot during the summer of 2020 by species into five height/diameter classes: (1) < 0.3 m, (2) 0.3–0.6 m, (3) 0.61–0.9 m, (4) 0.91–1.36 m, and (5) ≥ 1.37 m tall and < 3.8 cm DBH. DBH was recorded for all stems in class 5.

Substrate, Fuels, and Soil Sampling

To assess the relationship between forest substrate and regeneration, we followed the methods of Brown (1974) and Brown et al. (1982), to measure dead and down woody biomass along four 12.6 m transects in each 0.047 ha overstory plot for all treatments in the summer of 2020. Fine woody biomass (FWB) included 1-h (< 0.6 cm), 10-h (0.6–2.53 cm), and 100-h (2.54 to 7.6 cm) fuels. Coarse woody biomass (CWB, 1,000-h fuel) was downed wood > 7.6 cm in diameter. We tallied 1- and 10-h fuels along the first 1.3 m section, 100-h fuels along 3.5 m, and 1,000-h fuels along the entire length of each transect. For 1,000 h fuels, we recorded diameter at point of intersection to the nearest 0.1 cm, decay class (1–5, Lutes et al. 2006), and position (on vs. above the ground). Along each fuel transect at 3.1, 6.1, and 9.1 m (total of 12 measurements per plot), we measured the depth of the litter and duff layers to the nearest 0.25 cm and estimated the percent cover of leaf litter, duff, and bare ground within a 0.5 m^2 (70.6 × 70.6 cm) frame.

Previous research found that soil chemical characteristics are correlated with the post-harvest distribution of oak and competing species within our study region (Swain et al. 2018). Therefore, along each fuel transect 5 m from plot center, we collected mineral soil down to 10 cm using a trowel, combining the four subsamples into a composite sample for each plot. Samples were sealed in plastic bags and stored in a freezer until they were shipped to Brookside Labs in New Bremen, OH for chemical analysis. As part of a standard package, Brookside Labs analyzed S (ppm), P (ppm), Ca (mg kg^{-1}), Mg (mg kg^{-1}), K (mg kg^{-1}), Na (mg kg^{-1}), B (mg kg^{-1}), Fe (mg kg^{-1}), Mn (mg kg^{-1}), Cu (mg kg^{-1}), Zn (mg kg^{-1}), and Al (mg kg^{-1}) by Mehlich III extraction (Mehlich 1984). Samples were also analyzed for pH, total exchange capacity (meq 100 g^{-1}), percent organic matter, Bray II P (mg kg^{-1}), total

N ($NO_3 + NH_4$; ppm), percent Ca, Mg, K, Na, H, and other bases (Bray and Kurtz 1945; Dahnke and Johnson 1990; McLean 1982; Ross and Ketterings 1995; Schulte and Hopkins 1996). Soil NO_3 and NH_4 were summed for total soil N.

Data Preparation

Summary statistics calculated for each plot included: (1) average fire temperature by height (0 or 30.5 cm; ^{O}C), (2) average char height (cm), (3) total live basal area (BA, m^2 ha^{-1}), (4) average percent canopy density, (5) reproduction stem density (per 100 m^2) by height class, (6) average CWB volume (m^3 ha^{-1}), and (7) average FWB volume (m^3 ha^{-1}). Total live BA was calculated per plot from DBH measurements of tagged overstory, midstory, and ingrowth trees. We calculated average CWB volume from collected CWB fuel measurements and FWB volume was calculated for each fine fuel class, then totaled together and averaged per plot (Harmon and Sexton 1996). For analyses of post-burn effects, the average change in litter and duff depth from 2018–2020 was calculated. Aspect was transformed to a linear scale ranging from 0–2, with 0 facing southwest and 2 facing northeast (Beers et al. 1966).

Final status was determined for each tagged seedling; two consecutive surveys of the seedling as dead or missing resulted in classification as a dead seedling. Data imputation was conducted for any missing or inaccurate measurements of seedling height and basal diameter based on growth rates calculated for prior or subsequent remeasurement intervals. Some seedling species were grouped together (hereafter, species groups) for analysis, based on study focus and abundance. Resulting analyzed species and groups were white oak, black oak (*Q. velutina*), northern red oak (*Q. rubra*), other oak spp. (chestnut oak [*Q. montana*], post oak, scarlet oak [*Q. coccinea*], blackjack oak [*Q. marilandica*]), hickory spp., sugar maple, red maple (*A. rubrum*), white ash (*Fraxinus americana*), sassafras (*Sassafras albidum*), ironwood (*Ostrya virginiana*), canopy other, and subcanopy other. The canopy other species group consisted of overstory trees such as tuliptree, black cherry (*Prunus serotina*), American elm (*Ulmus americana*), and blackgum (*Nyssa sylvatica*). The subcanopy other group consisted of shrubs and small trees such as eastern redbud (*Cercis canadensis*) and flowering dogwood (*Cornus florida*). Black cherry comprised 34% of the canopy other group for tagged seedlings, while eastern redbud made up 60% of the subcanopy other group. Black cherry also contributed 18% of the canopy other group in the regeneration data, while eastern redbud made up 25% of the subcanopy other group. Nomenclature followed the USDA PLANTS Database (USDA, NRCS 2022).

Statistical Analyses

Following inspection, highly skewed data were log-transformed to improve normality (Table S2). We also standardized some explanatory variables by dividing by the standard deviation to minimize differences between variable ranges (Table S2). To evaluate how the regeneration layer responded to differences in treatments, we fit multiple mixed-effects models on survival, resprouting response, height, and seedling density (R Core Team 2020). We fit binomial models (glm function, R stats package-version 4.4.1) to estimate survival (alive vs. death) since treatment using the final status of individual seedlings as the response. To test direct fire effects, we fit a binomial model on post-burn survival of tagged seedlings from the time period 2018–2021. We also fit another binomial model for overall survival across the entire time frame of the study (2010–2021). Binomial models were also fit to estimate individual resprout response (topkilled and resprouted vs. not topkilled and resprouted) after the burn in 2021. We fit a Poisson model (glm function, stats package) to estimate the number of resprouts of tagged seedlings after the burn in 2021. For tagged seedlings, linear models (lm function, stats package) were fit to estimate the tallest resprout height post-burn (2021). The explanatory variables included in these models were: pretreatment basal diameter, total live BA, average canopy density, mean char height, average maximum fire temperature, soil chemical characteristics (pH, total N, P, Al), percent slope, transformed aspect, average FWB and CWB volumes, litter and duff depths, species group, and treatment (Table S2). We also fit negative binomial models using the glm.nb function (MASS package; Venables and Ripley 2002) to estimate seedling density in 2020. A negative binomial model was used because the data were over-dispersed and did not fit a Poisson distribution. The same explanatory variables described above were used except for basal diameter, and with the addition of seedling height class (1–5). Models were produced with a backward stepwise algorithm (step function, stats package) and chosen based on the lowest AIC (Akaike information criterion; Akaike 1974), and then all models were tested for goodness-of-fit before interpretation. Tests used for goodness-of-fit included chi-square (pchisq function) for negative binomial and Poisson models, the Hosmer–Lemeshow Goodness of Fit (GOF) Test (hoslem_test function) for binomial models, and linear models were checked for normality (shapiro_test function), skewness (skewness function), and homogeneity (levene_test function). Wald Chi-square tests were used to determine significant explanatory variables. For post-hoc analysis, Tukey multiple pairs comparison tests (glht function, multcomp package, version 1.4–26; Hothorn et al. 2008) were run on significant main effects for all models.

We initially tested models with treatment unit and plot as random effects in LME4, but preliminary analyses found that these random effects were always zero, or near zero ($|x| < 0.0001$). Subsequent loglikelihood ratio tests of fully parameterized random-effects models found these effects to be nonsignificant. Therefore, for parsimony, we report only additive models. For all tests, $\alpha = 0.05$.

Non-metric multidimensional scaling (NMDS) ordination using Bray–Curtis dissimilarity within the metaMDS function (vegan package, version 2.6–8; Oksanen et al. 2019) was used to examine post-treatment compositional shifts in the regeneration layer (relative seedling density) between 2010 and 2020. We initially included data from 2018 in the NMDS, but stress was lowered by removing them from the analysis. Species with fewer than five occurrences between both years were excluded from analysis. A maximum of 100 iterations were allowed. The number of axes was determined by stress and a scree plot (McCune and Grace 2002) to maintain stress below 0.2 (Kruskal 1964). The envfit function (999 permutations) was used to fit environmental vectors onto the ordination and calculate correlation coefficients between environmental variables and axis values. Only environmental variables with p-values < 0.05 were displayed graphically.

We also implemented a Permutational Multivariate Analysis of Variance (PERMANOVA, 999 permutations) using the adonis function (Anderson 2001) to test whether the centroid or dispersion of year or treatment groups were different within the ordination. We tested the homogeneity of dispersion of the groups (functions: betadisper, anova, permutest) before reporting final PERMANOVA results. We also conducted a SIMPER test of pairwise comparisons of groups to identify the percentage each species contributed to the differences between treatments or years. For all tests, $\alpha = 0.05$.

Results

Fire Intensity and Severity

According to paint tag data, maximum fire temperatures at ground level ranged from 79.4 ^{O}C to above 661.1 ^{O}C with average plot temperatures ranging from 248.9 to 426.7 ^{O}C. Temperatures 30.5 cm above ground ranged from 79.4 ^{O}C to 426.7 ^{O}C with average plot temperatures ranging from 76.7 to 315.6 ^{O}C. Mean char heights averaged 37.2 cm (range 7.6–93.9 cm). Paint tag temperatures and char heights did not significantly differ across treatments (ANOVA, $p > 0.05$). The maximum temperatures recorded by the HOBO sensors ranged from 84 to 546.9 ^{O}C with an average of 206.7 ^{O}C. Temperatures above 100 ^{O}C (eight devices) were attained for an average of 61 consecutive seconds (range = 42–105 s).

Seedling Survival and Height Growth Since 2010

Between 2010 (pretreatment) and 2021 (post-fire), white oak survival rate averaged 57.5%, while other oak species averaged 70%. Maple species averaged 29–43% survival, while white ash and ironwood averaged 44% and 56% survival since 2010, respectively (Table 1b). Overall, survival rates decreased over time since 2010, with white oak, ironwood, and white ash having greater survival than sugar maple and sassafras (Fig. 2a). This trend was not seen in the shelterwood treatment that also received mechanical midstory removal; ironwood and sugar maple had higher survival rates post-burn (Fig. 2a). Variables significantly affecting overall seedling survival of all species in 2020 include pretreatment basal diameter (log transformed, 2010), total BA (2020), mean char height (standardized), total soil N, soil P, species group, and treatment ($p < 0.05$; Table S3).

When results are presented as odds ratio or change in odds (%) of survival vs. death, a unit increase in log-transformed seedling basal diameter (cm) increased the odds of survival by 71% ($p < 0.001$). Across species, an increase in total BA (m^2 ha^{-1}) reduced the odds of survival by 10.1% ($p < 0.001$), and one standard deviation (SD = 0.82) increase in mean char height reduced survival by 26.4% ($p < 0.01$) with all other factors held constant. An increase in total N (ppm) or P (mg kg^{-1})

Table 1 Seedling survival rates (mean and range, %) (A) two-year post-burn since 2018 and (B) since 2010 by species group in 2021. Statistical differences between groups are marked with superscripts according to a post-hoc Tukey test (α = 0.05). Total seedlings represents total seedlings per tree group across the study site

Species Group	A. Survival since 2018			B. Survival since 2010		
	Mean (Min–Max)	Total Seedlings		Mean (Min–Max)	Total Seedlings	
Acer rubrum	66.7 (50.0–100.0)	19	ab	42.6 (25.0–60.0)	28	abc
Acer saccharum	48.8 (25.0–100.0)	20	a	29.3 (20.0–60.0)	30	a
Canopy other	92.7 (50.0–100.0)	50	bc	65.8 (16.7–100.0)	77	cd
Carya spp.	98.6 (75.0–100.0)	52	bc	75.7 (20.0–100.0)	70	d
Fraxinus americana	71.5 (25.0–100.0)	61	ab	44.0 (20.0–100.0)	96	ac
Ostrya virginiana	75.6 (33.3–100.0)	55	ac	56.0 (20.0–100.00)	80	ac
Other *Quercus* spp.	94.2 (66.7–100.0)	29	bc	73.6 (33.3–100.0)	41	cd
Quercus alba	98.4 (66.7–100.0)	51	c	57.5 (20.0–100.0)	92	cd
Quercus rubra	100.0 (100.0–100.0)	34	bc	71.8 (40.0–100.0)	51	cd
Quercus velutina	95.3 (50.0–100.0)	50	bc	73.2 40.0–100.0)	67	bd
Sassafras albidum	81.3 (33.3–100.0)	17	ac	35.6 (20.0–60.0)	45	a
Subcanopy other	86.4 (33.3–100.0)	63	bc	60.8 (18.2–100.0)	97	cd

increased survival odds by 4% or 7.3%, respectively ($p < 0.05$). Seedling survival in 2021 followed similar trends with significant explanatory variables. In 2021, post-hoc tests revealed hickory species had greater odds of survival than red maple by a factor of 4.7 ($p < 0.05$; Table 1). Hickory spp., other oak spp., white oak, northern red oak, and black oak exhibited greater survival odds than sugar maple by factors of 12.9, 10.5, 7.3, 9.8, and 10.5, respectively ($p < 0.001$). Sassafras had decreased odds of survival compared to other oak spp., white oak, northern red oak, and black oak ($p < 0.001$; Table 1).

The shelterwood without midstory removal treatment had greater seedling survival than those with chemical removal by a factor of 2.5 and mechanical removal by a factor of 1.9 ($p < 0.01$; not shown). Overall, mean heights of most species displayed little change in height between 2010 and 2021 (Fig. 2b). In addition, most species displayed little change in seedling height after the 2019 prescribed burn, with the exception of ironwood. This species displayed a decrease in height across

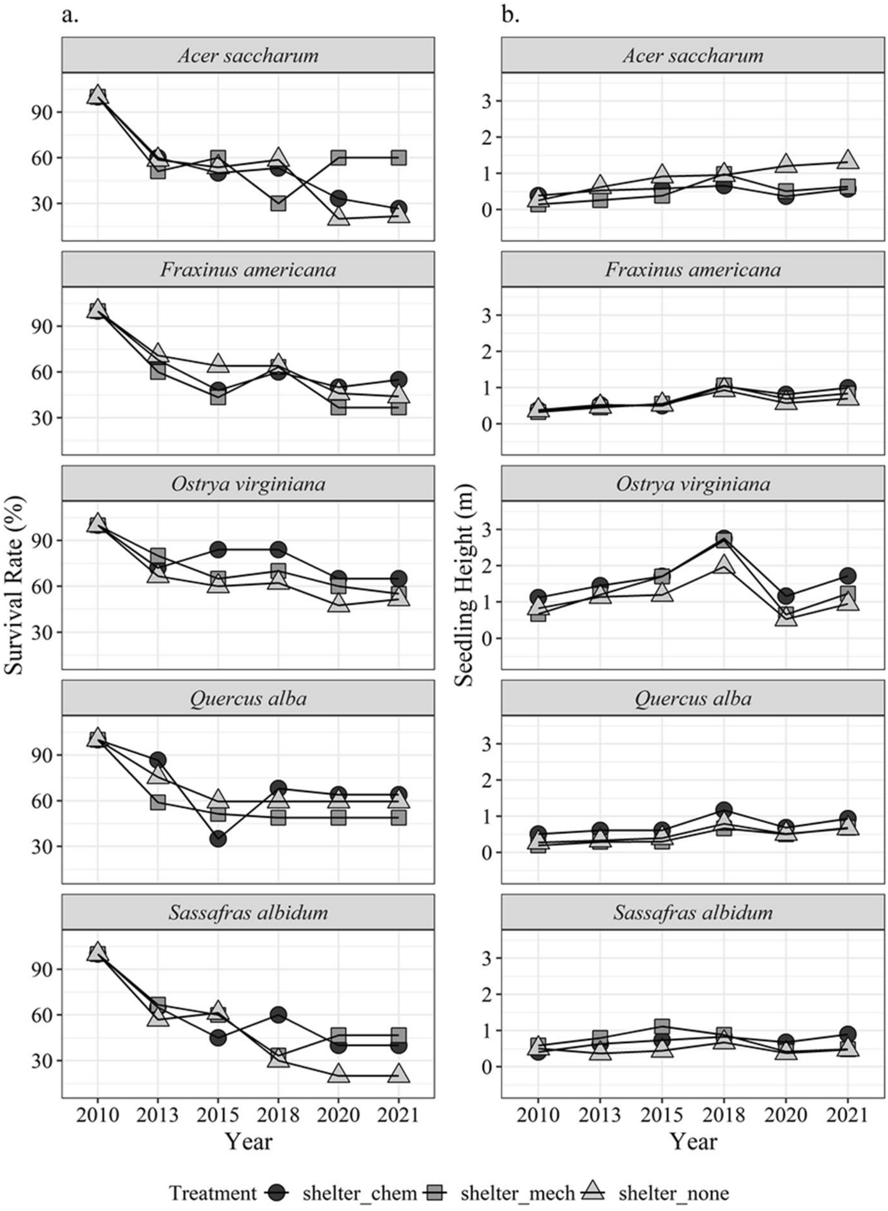

Fig. 2 **a** Survival rate (%) and **b** seedling height (m; mean) of the five most abundant tagged species from 2010 to 2021 by treatment. Shelter_chem = shelterwood with chemical midstory removal, shelter_mech = shelterwood with mechanical midstory removal, and shelter_none = shelterwood without midstory removal

treatments from 1.14 m in 2018 to 0.5 m in 2020. However, the mean height of ironwood rebounded to 0.80 m in the 2021 remeasurement.

Post-fire Seedling Survival

In 2021, oak and hickory seedlings averaged over 90% survival after the burn, while maple species seedling survival was less than 67%. White ash and iron wood also had lower average survival rates than oak species at 72 and 76%, respectively (Table 1a). Across all species, the 2021 post-burn survival model identified soil pH, species group, total N and average FWB as significant explanatory variables (2018, $p<0.05$; Table S3). A unit increase in pH decreased the odds of survival by 60% ($p<0.01$). A unit increase in total N (ppm) increased survival odds by 13% ($p<0.05$). An increase in a unit of FWB ($m^3\ ha^{-1}$) decreased the odds of survival by 9% ($p<0.05$). Post-hoc Tukey tests indicated that hickory spp., other oak, white oak, northern red oak, and black oak had significantly greater odds of survival than sugar maple by factors of 67.4, 29, 84.3, 47.3, and 20.2, respectively ($p<0.05$; Table 1a). White oak exhibited greater survival odds post-fire than white ash by a factor of 37.2 ($p<0.05$).

Resprouting Rate and Response

Oak seedlings displayed vigorous sprouting, with mean post-burn resprout rates of 92.5% and above for oak species in 2021, compared to maple species which resprouted at a rate of 66.7% or lower (Table 2). White ash and ironwood also had lower resprout responses than oak species (Table 2). Resprouting response in 2021 was significantly affected by species group, pH, FWB (2018), and litter depth change ($p<0.05$; Table S4). A unit increase in pH decreased the odds of resprouting by 50% and an increase in total FWB ($m^3\ ha^{-1}$) decreased resprouting odds by

Table 2 Two-year post-burn resprout rates since 2018 (mean and range, %) by species group in 2021. Statistical differences between groups are marked with superscripts according to a post-hoc Tukey test ($\alpha=0.05$). Total seedlings represents total seedlings per tree group across the study site

Species Group	Mean	Min	Max	Total Seedlings	
Acer rubrum	66.7	50.0	100.0	19	ac
Acer saccharum	51.4	25.0	100.0	17	a
Canopy other	93.2	66.7	100.0	48	bc
Carya spp.	95.8	50.0	100.0	52	bc
Fraxinus americana	71.5	25.0	100.0	61	ab
Ostrya virginiana	69.9	33.3	100.0	55	ac
Other *Quercus* spp.	94.2	66.7	100.0	29	bc
Quercus alba	98.4	66.7	100.0	51	c
Quercus rubra	98.2	75.0	100.0	34	bc
Quercus velutina	92.5	25.0	100.0	50	bc
Sassafras albidum	81.3	33.3	100.0	17	ac
Subcanopy other	66.7	50.0	100.0	19	ac

9% (p < 0.05). A unit increase in litter depth change (i.e., reduced litter depth; cm) increased the odds of resprouting by a factor of 2.0. In 2021, post-hoc Tukey tests showed that hickory spp., other oak spp., white oak, northern red oak, and black oak all had greater odds of resprouting than sugar maple by factors of 30.1, 35.8, 111.7, 36.2, and 18, respectively (p < 0.01; Table 2). The mean number of oak resprouts per stem in 2021 was 2.7 (range 1–7) compared to Acer spp. with 2.9 (range 1–6) and white ash with 3.1 resprouts (range 1–11).

In 2021, resprout counts were significantly affected by basal diameter (log-transformed, 2018), soil Al (standardized), FWB (2018), species group and treatment (p < 0.05; Table S4). With one unit increase in log basal diameter, the expected number of resprouts increased by a factor of 1.4 (p < 0.001), with all other variables fixed. An increase in standard deviation (SD = 0.97) of soil Al increased the expected resprout count by a factor of 1.1 (p < 0.001) with all other variables fixed.

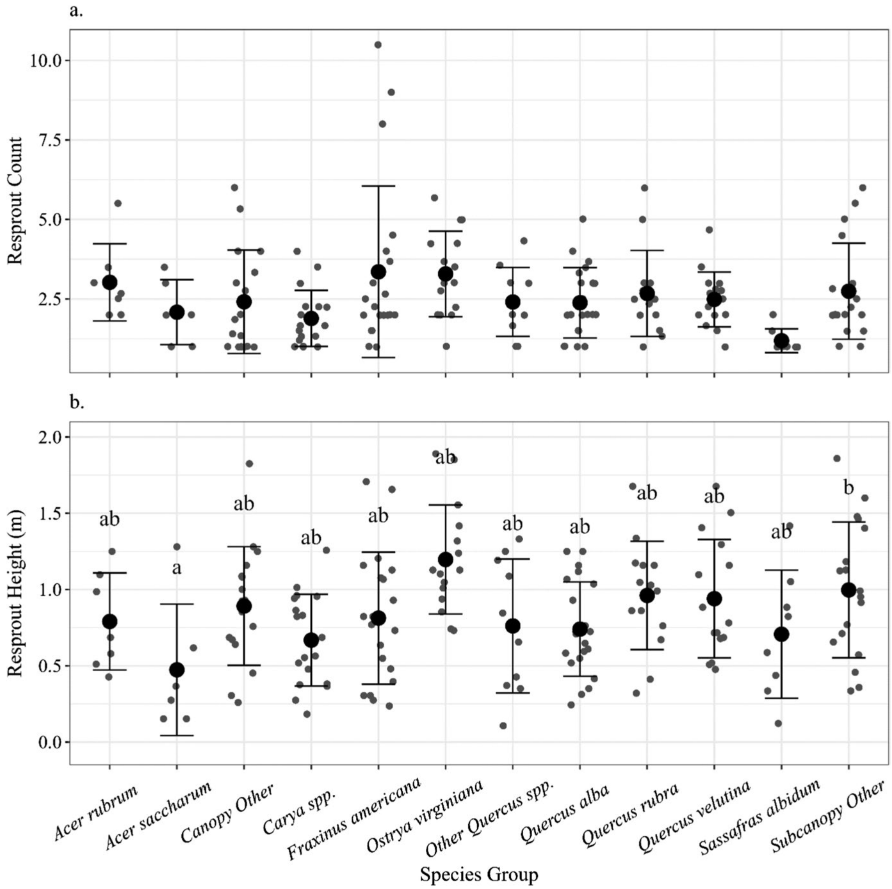

Fig. 3 **a** Resprout count and **b** height (m; mean ± SD) by species groups post-burn in 2021. Superscripts denote significant differences of resprout heights between species groups according to a post-hoc Tukey test (α = 0.05)

With a unit increase in FWB ($m^3\ ha^{-1}$), the expected number of resprouts decreased by a factor of 0.97 ($p<0.05$). Significant differences between species group and treatment groups were not detected in 2021 post-hoc Tukey tests ($p>0.05$, Fig. 3a).

Resprout Height

In 2020, the average height of oak resprouts was 0.67 m (0.09–1.98) and increased to 0.92 m (0.12–2.74 m) in 2021. Maple and white ash heights averaged 0.53 and 0.66 m and increased to 0.68 and 0.86 m in 2021. Ironwood resprouts averaged 0.62 m (0.09–1.4) in 2020 and increased to 1.2 m (0.3–2.1) in 2021. In 2021, resprout heights were significantly affected by basal diameter (log-transformed, 2018), total soil N, total BA (log-transformed, 2018), and average canopy density (standardized, 2018; $R^2=0.4657$, $p<0.05$). Every increase in log BA decreased log resprout height by 0.28 log m and every one standard deviation increase for canopy density (SD = 0.85) decreased log resprout height by 0.1 log m ($p<0.01$). Subcanopy Other mean resprout height was 0.68 log m greater than sugar maple ($p<0.05$) with no differences detected between other species group pairs (Fig. 3b). Post-hoc Tukey tests did not detect significant differences between treatment groups, but the model showed that shelterwood treatments with and without mechanical midstory removal exhibited 0.18 and 0.17 greater log m resprout height, respectively, than shelterwood with chemical midstory removal ($p<0.05$).

Reproduction Density

Pre-burn, white oak averaged 4,890 stems ha^{-1} and then doubled to 9,860 stems ha^{-1} post-burn. Comparatively, white ash and ironwood increased from approximately 8,710 and 3,900 stems ha^{-1} to 11,330 and 6,890 stems ha^{-1} after the burn. In 2020 (post-burn), seedling density was significantly affected by height class (1–5), species group, mean char height (standardized), total soil N, transformed aspect, FWB in 2018, and treatment ($p<0.05$; Table S4). An increase in one standard deviation of char height (SD = 1) decreased the number of seedlings by a factor of 0.87, while an increase in N (ppm) increased the number of seedlings by a factor of 1.03 ($p<0.001$). A unit increase in transformed aspect decreased seedling density by a factor of 0.60 ($p<0.05$). The density of seedlings also decreased with an increase in FWB ($m^3\ ha^{-1}$) by a factor of 0.97 ($p<0.001$), with all other variables held constant. Post-hoc Tukey tests indicated shelterwood without midstory removal had a greater post-burn abundance of seedlings than shelterwood with chemical midstory removal by a factor of 1.4 ($p<0.01$; Fig. 4). Differences between species groups were detected with white oak, ironwood, and white ash having a greater abundance of seedlings than red maple ($p<0.001$; Fig. 4). Northern red and black oak had significantly fewer seedlings than white ash ($p<0.001$). Other oak species, northern red oak and black oak had significantly fewer seedlings than ironwood ($p<0.001$; Fig. 4). Across all species groups, there were significantly fewer seedlings in the taller height classes (4 and 5) compared to the shorter classes (classes 1, 2, and 3; $p<0.001$; Fig. 5).

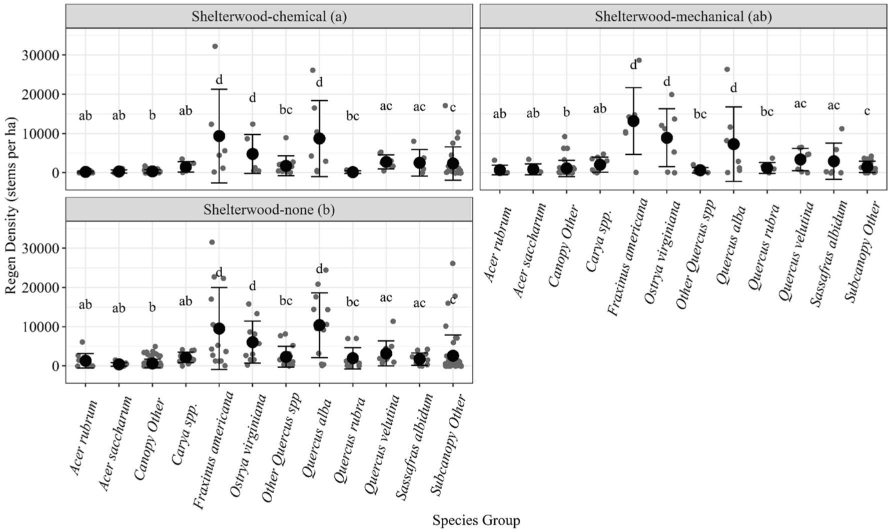

Fig. 4 Regeneration density (stems ha^{-1}; mean ± SD) by treatments post-burn in 2020. Superscripts indicate significant differences between species groups and treatment groups according to a post-hoc Tukey test (α = 0.05). Shelterwood-chemical = shelterwood with chemical midstory removal, Shelterwood-mechanical = shelterwood with mechanical midstory removal, and Shelterwood-none = shelterwood without midstory removal

NMDS Ordination

The NMDS of regeneration-layer species resulted in a two-dimensional solution and stress of 0.164 (linear $R^2 = 0.869$). Environmental and stand variables that were significantly correlated with the ordination included post-harvest BA, mean char height, pH, soil organic matter, Al concentration, total N, average canopy density in 2020, and percent slope ($p < 0.05$), with pH ($R^2 = 0.56$, $p = 0.001$) and Al ($R^2 = 0.59$, $p = 0.001$) exhibiting the strongest correlations (Table 3, Fig. 6a). NMDS axis 1 was strongly related to site and stand characteristics such as pH, Al, total N, organic matter, average canopy density, and BA (Fig. 6a). NMDS axis 2 was strongly related to fire severity (mean char height) as well as the percent slope (Fig. 6a). Relative abundance of white ash and sugar maple was correlated with more productive soils, while several oak species were correlated higher soil Al concentrations (Fig. 6a). The fire treatment pushed species composition from sugar maple and white ash to greater relative abundance of white and black oak (Fig. 6a). Plots from 2010 were associated with a higher relative abundance of maple species and sassafras, while 2020 plots were associated with higher relative abundances of white oak, black oak, and hickory species. (Fig. 6b). While there was overlap in the distribution of plots between years 2010 and 2020, there was a clear grouping between the two years (Fig. 6b). There was a high degree of overlap between treatment groups, especially shelterwood with mechanical midstory removal and without midstory removal (Fig. 6c). The shelterwood with mechanical midstory removal does not appear

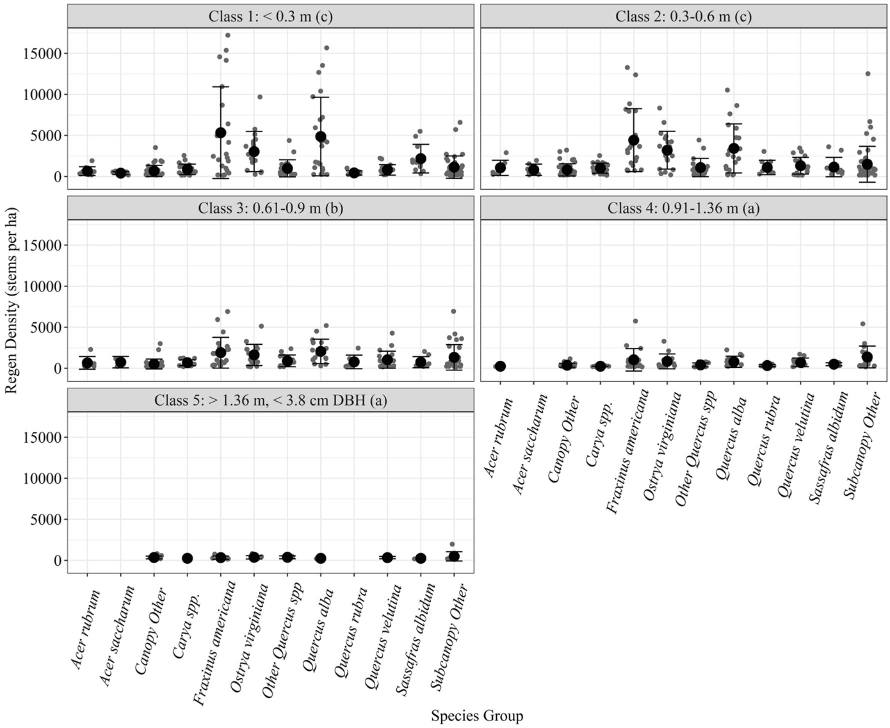

Fig. 5 Regeneration density (stems ha^{-1}; mean ± SD) by height class (1–5) in 2020. Superscripts denote significant differences between height classes according to a post-hoc Tukey test (α = 0.05)

to have been conducted across the entire environmental gradient at the site, as the grouping does not span axis 1 (Fig. 6c). Shelterwood without midstory removal was distributed across the environmental gradient represented by axis 1, while shelterwood with chemical midstory removal was distributed across axis 2 towards the portion of the ordination associated with greater char height and Al concentration (Fig. 6c). Between 2010 and 2020, most plots on the right side of the ordination exhibited compositional shifts away from red maple and sassafras towards greater importance of post and white oak along axis 2 (Fig. 6d), the axis most strongly associated with increased char height and decreasing percent slope (Fig. 6a). However, plots on the left side of the ordination displayed smaller compositional shifts in multiple directions, which was associated with sugar maple and white ash and greater soil productivity and residual density of canopy trees (Fig. 6d). The PERMAVONA did not detect significant differences among treatments, but did detect a significant difference between 2010 and 2020 ($p < 0.05$). The SIMPER test indicated that sassafras, white ash, and white oak were the top three contributors of differences between 2010 and 2020, contributing 17, 16, and 13%, respectively.

Table 3 Correlation coefficients and p-values (bold: $p < 0.05$) for selected environmental variables with NMDS ordination of regeneration density data

Environmental Variable	R^2	P-value
BA (2010)	0.086	0.118
BA (2018)	**0.138**	**0.035**
BA (2020)	0.119	0.053
High Mean Temp (30.5 cm)	0.085	0.131
Low Mean Temp (0 cm)	0.060	0.251
Mean Char Height	**0.251**	**0.005**
pH	**0.564**	**0.001**
% Organic Matter	**0.376**	**0.001**
P (mg kg-1)	0.120	0.057
Al (mg kg-1)	**0.587**	**0.001**
Total N (ppm)	**0.167**	**0.014**
Canopy Density (2018)	0.090	0.124
Canopy Density (2020)	**0.312**	**0.002**
Canopy Density (2010)	0.036	0.43
CWB (2018)	0.081	0.156
CWB (2020)	0.078	0.183
FWB (2018)	0.058	0.25
FWB (2020)	0.099	0.079
Litter Depth (2018)	0.011	0.76
Duff Depth (2018)	0.045	0.345
Litter Depth (2020)	0.068	0.209
Duff Depth (2020)	0.029	0.481
Litter Change (2018–2020)	0.115	0.066
Duff Change (2018–2020)	0.037	0.435
Transformed Aspect	0.013	0.753
% Slope	**0.169**	**0.012**
Average TSI	0.030	0.498

Discussion

To achieve sufficient oak regeneration, managers often combine harvests with prescribed burns, with more productive sites typically requiring more burns than less productive sites (Iverson et al. 2008). One of our objectives was to assess whether a shelterwood harvest on a less productive site would achieve competitive oak reproduction following a single prescribed burn. After a single burn, we observed greater survival and resprouting of oak seedlings compared to competitors (question 1). Shelterwood studies conducted on more productive sites (SI_{50} 23 m vs. 17.6 m in our study) have also observed lower mortality of oak seedlings compared to competitors following burning (Brose et al. 1999b; Brose 2010). Generally, oak species maintained higher survival rates with increasing burn intensity compared to competing species such as red maple and tuliptree (Brose and Van Lear 1998; Brose 2010). We observed greater oak seedlings survival post-burn than maple species and white ash,

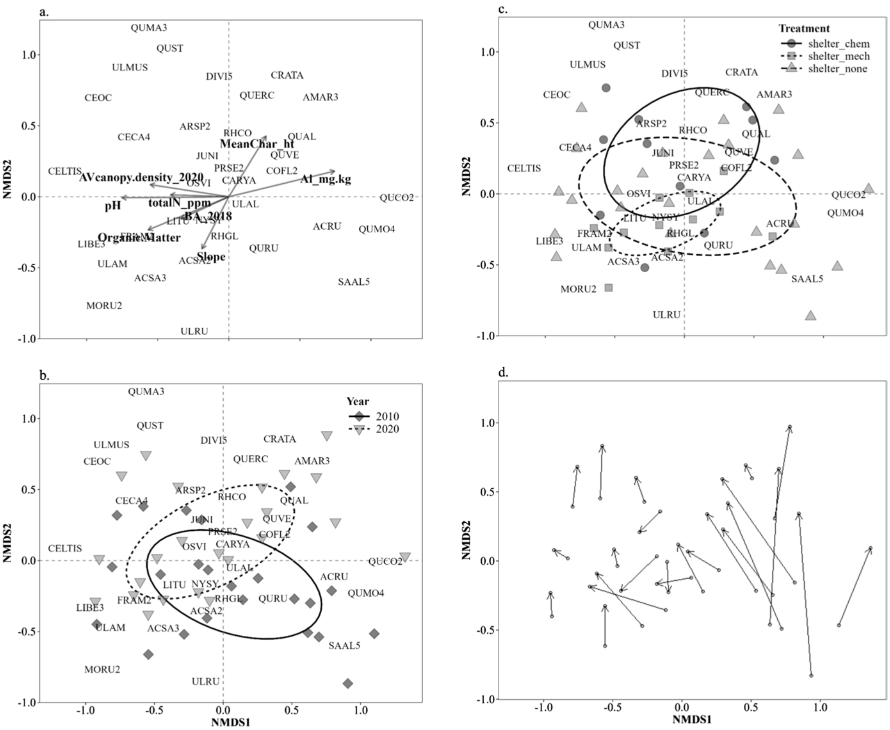

Fig. 6 NMDS ordination of regeneration-layer species composition in 2010 and 2020: **a** Biplot of regeneration species with significant ($p < 0.05$) environmental factors MeanChar_ht (mean char height), Al_mg.kg (soil Al), Slope (percent slope), BA_2018 (basal area in 2018), Organic.Matter (percent soil organic matter), totalN_ppm (total soil N), pH (soil pH), and AVcanopy.density_2020 (average canopy density in 2020) as vector arrows; **b** Biplot of regeneration plots and species grouped by years 2010 and 2020; **c** Biplot of regeneration plots and species grouped by silvicultural treatments shelter_chem (shelterwood with chemical midstory removal), shelter_mech (shelterwood with mechanical midstory removal), and shelter_none (shelterwood without midstory removal); **d** Successional vector changes of regeneration composition moving from years 2010 to 2020. Species abbreviations: ACRU = *Acer rubrum*, ACSA2 = *Acer saccharinum*, ACSA3 = *Acer saccharum*, AMAR3 = *Amelanchier arborea*, ARSP2 = *Aralia spinosa*, CARYA = *Carya* spp., CECA4 = *Cercis canadensis*, CELTIS = *Celtis* spp., CEOC = *Celtis occidentalis*, COFL2 = *Cornus florida*, CRATA = *Crataegus* spp., DIVI5 = *Diospyros virginiana*, FRAM2 = *Fraxinus americana*, JUNI = *Juglans nigra*, LIBE3 = *Lindera benzoin*, LITU = *Liriodendron tulipifera*, MORU2 = *Morus rubra*, NYSY = *Nyssa sylvatica*, OSVI = *Ostrya virginiana*, PRSE2 = *Prunus serotina*, QUAL = *Quercus alba*, QUCO2 = *Quercus coccinea*, QUERC = *Quercus* spp., QUMA3 = *Quercus marilandica*, QUMO4 = *Quercus montana*, QURU = *Quercus rubra*, QUST = *Quercus stellata*, QUVE = *Quercus velutina*, RHCO = *Rhus copallinum*, RHGL = *Rhus glabra*, SAAL5 = *Sassafras albidum*, ULAL = *Ulmus alata*, ULAM = *Ulmus americana*, ULMUS = *Ulmus* spp., ULRU = *Ulmus rubra*

the main competitors at our site. A meta-analysis conducted by Brose et al. (2013) also found oak seedlings resprouted at a higher rate than mesophytic species following burning, particularly when seedlings were released from competition. Studies of controlled basal heating or burning on seedlings also found higher resprouting rates in oak compared to maple species (Huddle and Pallardy 1996; Keyser 2019). In our study, increased FWB volume was associated with a 9% decrease in resprouting odds across all species, suggesting that increased fuels, as represented by FWB, may be associated with decreased sprouting of fire sensitive species.

Following the shelterwood and burn in our study, oak seedlings doubled in density and were more abundant than most competitors. Following shelterwood harvests and burning, Brose et al. (1999b) observed 1,709 oak stems ha^{-1} for low-medium intensity, 2,385 stems ha^{-1} for medium–high intensity, and 4,160 stems ha^{-1} for high intensity burns. Our burn, with an average temperature of 195^{0} C (77–315^{0} C) measured at 30 cm, was most comparable to the low-medium intensity burn observed in Brose et al. (1999b) with temperatures 135–200^{0} C measured at 1 m. Because Brose et al. (1999b) counted all stems originating from one root system as one individual and we counted each stem, we divided our oak densities by the average number of oak resprouts (2.8 resprouts per stem) to allow comparison to their densities. In comparison, densities of oak seedlings $\geq$ 0.3 m tall in our study averaged 3,522 stems ha^{-1} which are more comparable to the higher intensity burn densities (4,160 stems ha^{-1}) seen in Brose et al. (1999b) on a more productive site.

While seedlings of all species were abundant after burning, they were generally less than 0.9 m tall, regardless of species. Within these height classes (1–3), oak species comprised of 34% of stems, compared to 23% for white ash, 6% for sassafras, and 4% for maple species (data not shown). Thus, oaks made up a large proportion of the regeneration layer and had greater or comparable relative abundance compared to competitors. While our results suggest that oak seedlings are competitive with those of other species, differences in metrics used to assess competitive seedlings make comparison to field standards difficult. According to Sander et al. (1976), 1,070 stems ha^{-1} (height > 1.37 m) are needed to attain a minimum of 30% BA of oak in the future overstory in the Missouri Ozarks. According to the HNF silvicultural guidelines, approximately 988 competitive oak-hickory stems per ha are desired by the end of the fifth growing season post-treatment on lower quality sites. Competitive seedlings are defined as being 80% of the height of the nearest competitor. Two years post burn, we observed over 3,500 oak stems ha^{-1} ($\geq$ 0.3 m) and they had comparable densities to their main competitors across height classes.

Several studies have found a correlation between larger pre-burn seedlings and increased survival, resprout density, and resprout height (Dey and Hartman 2005; Keyser 2019). We also found larger pre-burn basal diameter was associated with better odds of post-burn survival, greater number of resprouts, and greater resprout and seedling height. Because the harvest in our study was conducted over a multi-year period, some of the seedlings in our study had shorter release periods following harvest, and a shorter post-release period may have resulted in lower basal diameter growth of some of our tagged seedlings.

In our study, species compositional shifts from species such as red maple and sassafras toward greater importance of oaks were observed in the NMDS ordination on plots associated with lower soil productivity (higher Al, lower pH). These plots were influenced to a greater extent by the fire treatment (char height) compared to plots associated with greater soil productivity (greater N, organic matter, and pH) and mesophytic species such as sugar maple and white ash. Composition on these more productive plots shifted in multiple directions, indicating no clear change and suggesting the fire did not drive composition toward greater oak importance. This is consistent with lower productivity sites retaining more oak and shifting more readily away from mesophytic species with the application of fire (Hutchinson et al. 2005; Burton et al. 2010).

Topographic factors influenced species composition and response to treatments. Steeper slopes were associated with increased survival and resprouting odds, while east-northeasterly sites displayed decreased survival and resprouting odds and lower seedling abundance. The greater abundance of oak seedlings we observed in our study likely resulted from their ability to establish and persist on the drier conditions of southwest-facing slopes (Quackenbush 2016; Swaim et al. 2018). In addition, the xeric conditions of these aspects interact with steeper slopes to produce greater burn severity, which favors oaks due to their adaptations to fire. Even though we observed greater survival on steeper slopes, greater densities of most oak species were associated with less steep slopes in our ordination analysis. This is consistent with other studies that found higher oaks densities on less-steep slopes and lower densities on steeper slopes (Cuprewich and Saunders 2023). Although we saw a strong shift in species composition of the regeneration layer that was associated with harvest and fire treatments, seedlings were still influenced by site and other environmental variables. Because our study site is on the lower end of the productivity and moisture gradient associated with oak-dominated forests in southern Indiana, the site was predisposed to favor oak species and disfavor the heavy establishment of mesophytic species. Therefore, less intense, and infrequent fire may be used to favor oaks on these sites where conditions may act as a filter to reduce the abundance and vigor of mesophytic competitors. With limited days where conditions (weather and site) allow the application of prescribed fire to meet management objectives in the study area, it is likely that sites like these, where objectives have been met, will be burned less frequently, if at all, due to other management priorities.

We expected seedlings within the shelterwood without midstory removal to have reduced survival, shorter heights, and lower densities due to increased shading compared to other treatments (question 2). However, seedlings had greater survival odds across all species without midstory removal compared to both midstory removal treatments. In addition, seedling density was higher in shelterwood without midstory removal compared to chemical midstory removal. Hackworth et al. (2020) observed taller oak seedlings in a midstory removal conducted nine years prior to a shelterwood harvest, however, the midstory removal treatment also displayed reduced frequency of free-to-grow oaks (relative to understory competitors) compared to an untreated control. In our study, the timing of midstory removals varied relative to shelterwood treatments, with shelterwood harvests occurring 0–3 years prior to midstory treatments. In a study with shelterwood harvest and midstory removal occurring within a year of each other, no differences in oak seedling density were observed between shelterwood treatments with and without midstory removal, but the midstory removal treatment did exhibited greater seedling growth (Cunningham 2015). Further study is needed to determine how the timing of midstory and shelterwood treatments affect the establishment and growth of oak seedlings.

Conclusions

Our study found a shelterwood treatment combined with a single burn on a less productive site had positive effects on oak regeneration relative to competing species. However, contrary to our predictions, midstory treatments did not favor the growth or survival of oak seedlings. With the high post-fire survival and resprouting of oaks, in addition to increased abundance, one burn may be sufficient to promote adequate reproduction of competitive seedlings. The greater tolerance of oak species to low moisture and nutrient availability (Kabrick et al. 2014) allows persistence on less productive sites. Evaluation of oak seedling densities and competitive status should continue to confirm sufficient densities of competitive seedlings remain to meet recommended levels. The final removal cut of the shelterwood may promote changes in competition that require additional prescribed fire or crop tree thinning to maintain oak at desired stocking.

Successfully regenerating oak species can be both time-consuming and costly. However, if less productive sites can produce sufficient oak seedlings with a single burn following a shelterwood harvest, it is less costly to manage these less productive sites. While these sites may have lower value timber, continuing to maintain their oak dominance will provide vital ecological services. Over 70% of the HNF is oak-hickory forest, and as such, its forests are representative of much of the Central Hardwood Region (Woodall et al. 2007). This wide distribution of xeric oak-dominated forests offers an opportunity to efficiently manage for this ecologically valuable forest type across the region.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s44391-025-00022-y.

Acknowledgements We thank Steve Harriss, Terry Severson, and the Forest Service burn crew. Sarah Palmer, Alexander Johnson, Bill Mullins, Lucas Voorhees, Adam George, Carrie Baker, Jessica Schaner, Michelle McKee, Samuel Tourellot, and David Mann assisted with field sampling. The Purdue Statistical Consulting Services, Yujie Chen, Arman Sabbaghi, Bruce Craig, Ben Rivera, and Sarah Cuprewich provided invaluable guidance with analyses.

Author Contribution Conceptualization: DC Dey, MA Jenkins, JM Kabrick, MR Saunders, JT Swaim, CD Thornton; Methodology: DC Dey, MA Jenkins, JM Kabrick, MR Saunders, JT Swaim, CD Thornton; Formal analysis and investigation: MA Jenkins, RWE Quackenbush, SJ Rademacher; Writing—original draft preparation: SJ Rademacher; Writing—review and editing: DC Dey, MA Jenkins, JM Kabrick, RWE Quackenbush, SJ Rademacher, MR Saunders, JT Swaim, CD Thornton; Funding acquisition: MA Jenkins, CD Thornton; Resources: MA Jenkins, JT Swaim, CD Thornton; Supervision: MA Jenkins.

Funding Funding was provided by the USDA Forest Service.

Data Availability Data will be made available upon request.

Declarations

Ethics Approval None to declare.

Consent to Participate Not applicable.

Conflict of Interest The authors declare no conflicts of interest.

References

Abrams, M.D. 1992. Fire and the development of oak forests. *BioScience* 42: 346–353. https://doi.org/10.2307/1311781.

Abrams, M.D., and J.A. Downs. 1990. Successional replacement of old-growth white oak by mixed mesophytic hardwoods in southwestern Pennsylvania. *Canadian Journal of Forest Research* 20: 1864–1870. https://doi.org/10.1139/x90-250.

Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19 (6): 716–723. https://doi.org/10.1109/TAC.1974.1100705.

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x.

Beers, T.W., P.E. Dress, and L.C. Wensel. 1966. Notes and observations: Aspect transformation in site productivity research. *Journal of Forestry* 64: 691–692. https://doi.org/10.1093/jof/64.10.691.

Bray, H.R., and L.T. Kurtz. 1945. Determination of total, organic, and available forms of phosphorus in soils. *Soil Science* 59: 39–45. https://doi.org/10.1097/00010694-194501000-00006.

Brose, P.H. 2010. Long-term effects of single prescribed fires on hardwood regeneration in oak shelterwood stands. *Forest Ecology and Management* 260: 1516–1524. https://doi.org/10.1016/j.foreco.2010.07.050.

Brose, P.H., and D.H. Van Lear. 1998. Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. *Canadian Journal of Forest Research* 28: 331–339. https://doi.org/10.1139/x97-218.

Brose, P.H., D.H. Van Lear, and P.D. Keyser. 1999a. A shelterwood—burn technique for regenerating productive upland oak sites in the Piedmont region. *Southern Journal of Applied Forestry* 23: 158–163. https://doi.org/10.1093/sjaf/23.3.158.

Brose, P.H., D.H. Van Lear, and R. Cooper. 1999b. Using shelterwood harvests and prescribed fire to regenerate oak stands on productive upland sites. *Forest Ecology and Management* 113: 125–141. https://doi.org/10.1016/S0378-1127(98)00423-X.

Brose, P.H., D.C. Dey, R.J. Phillips, and T.A. Waldrop. 2013. A meta-analysis of the fire-oak hypothesis: Does prescribed burning promote oak reproduction in eastern North America? *Forest Science* 59: 322–334. https://doi.org/10.5849/forsci.12-039.

Brose, P.H., D.C. Dey, and T.A. Waldrop. 2014. *The fire-oak literature of eastern North America: Synthesis and guidelines*. NRS-GTR-135. Newtown Square, PA: USDA Forest Service, Northern Research Station, p. 98. https://doi.org/10.2737/NRS-GTR-135.

Brown, J.K., R.D. Oberheu, and C.M. Johnson. 1982. *Handbook for inventorying surface fuels and biomass in the interior west.* Rep. No. GTR INT-129. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. https://doi.org/10.2737/INT-GTR-129.

Brown, J.K. 1974. *Handbook for inventorying down woody material.* General Technical Report INT-16. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 24 p. https://research.fs.usda.gov/treesearch/28647.

Burton, J.A., S.W. Hallgren, and M.W. Palmer. 2010. Fire frequency affects structure and composition of xeric forests of eastern Oklahoma. *Natural Areas Journal* 30: 370–379. https://doi.org/10.3375/043.030.0401.

Craig, J.M., J.M. Lhotka, and J.W. Stringer. 2014. Evaluating initial responses of natural and underplanted oak reproduction and a shade-tolerant competitor to midstory removal. *Forest Science* 60: 1164–1171. https://doi.org/10.5849/forsci.13-602.

Cunningham, K.K. 2015. Third-year response of oak natural reproduction to a shelterwood harvest and midstory competition control in the Arkansas Ozarks. In *Proceedings of the 17th Biennial Southern Silvicultural Research Conference*, Shreveport, LA, USA, 5–7: 5–12.

Cuprewich, S.A., and M.R. Saunders. 2023. Evaluating the impact of prescribed surface fire on seedlings in the Central Hardwood Region, USA. *Forestry* 97: 94–106.https://doi.org/10.1093/forestry/cpac064.

Dahnke, W.C., and G.V. Johnson. 1990. Testing soils for available nitrogen. In *soil testing and plant analysis, SSSA Book Series,* ed. by R.L. 127–139. Westerman, Madison, WI: Soil Science Society of America. https://doi.org/10.2136/sssabookser3.3ed.c6.

Dey, D.C. 2014. Sustaining oak forests in eastern North America: Regeneration and recruitment, the pillars of sustainability. *Forest Science* 60: 926–942. https://doi.org/10.5849/forsci.13-114.

Dey, D.C., and G. Hartman. 2005. Returning fire to Ozark Highland forest ecosystems: Effects on advance regeneration. *Forest Ecology and Management* 217: 37–53. https://doi.org/10.1016/j.foreco.2005.05.002.

Hackworth, Z.J., J.M. Lhotka, and J.W. Stringer. 2020. Midstory removal facilitates growth but reduces competitiveness of oak reproduction prior to and after shelterwood establishment cutting. *Forest Science* 66: 371–381. https://doi.org/10.1093/forsci/fxz083.

Hanberry, B.B., and G.J. Nowacki. 2016. Oaks were the historical foundation genus of the east-central United States. *Quaternary Science Reviews* 145: 94–103. https://doi.org/10.1016/j.quascirev.2016.05.037.

Hanberry, B.B., D.C. Dey, and H.S. He. 2014. The history of widespread decrease in oak dominance exemplified in a grassland–forest landscape. *Science of the Total Environment* 476–477: 591–600. https://doi.org/10.1016/j.scitotenv.2014.01.048.

Harmon, M.E., and J. Sexton. 1996. *Guidelines for measurements of woody debris in forest ecosystems*. Pub. No. 20. Seattle, WA: US LTER Network Office, University of Washington. pp. 73. https://digitalrepository.unm.edu/lter_reports/148.

Harriss, S. 2019. *Jeffries prescribed burn silviculture monitoring.* Hoosier National Forest, Tell City, IN.

Homoya, M.A., D.B. Abrell, J.R. Aldrich, and T.W. Post. 1985. The natural regions of Indiana. *Proceedings of the Indiana Academy of Science* 94: 245–268.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* 50: 346–363. https://doi.org/10.1002/bimj.200810425.

Huddle, J.A., and S.G. Pallardy. 1996. Effects of soil and stem base heating on survival, resprouting and gas exchange of *Acer* and *Quercus* seedlings. *Tree PhysiolOgy* 16: 583–589. https://doi.org/10.1093/treephys/16.6.583.

Hutchinson, T.F., E.K. Sutherland, and D.A. Yaussy. 2005. Effects of repeated prescribed fires on the structure, composition, and regeneration of mixed-oak forests in Ohio. *Forest Ecology and Management* 218: 210–228. https://doi.org/10.1016/j.foreco.2005.07.011.

Iverson, L.R., T.F. Hutchinson, A.M. Prasad, and M.P. Peters. 2008. Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern U.S.: 7-year results. *Forest Ecology and Management* 255: 3035–3050. https://doi.org/10.1016/j.foreco.2007.09.088.

Jenkins, M.A., and G.R. Parker. 1998. Composition and diversity of woody vegetation in silvicultural openings of southern Indiana forests. *Forest Ecology and Management* 109: 57–74. https://doi.org/10.1016/S0378-1127(98)00256-4.

Jenkins, M.A. 2013. The history of human disturbance in forest ecosystems of southern Indiana. In *The hardwood ecosystem experiment: A framework for studying responses to forest management*. ed. by R.K. Swihart, M.R. Saunders, R.A. Kalb, S. Haulton, and C.H. Michler, 2–11. General Technical Report NRS-P-108. Newtown Square, PA: USDA Forest Service, Northern Forest Experiment Station. https://research.fs.usda.gov/treesearch/42896.

Johnson, P.S., S.R. Shifley, R. Rogers, D.C. Dey, and J.M. Kabrick. 2019. *The ecology and silviculture of Oaks*, 3rd ed. London, UK: CABI Publishing.

Kabrick, J.M., J.L. Villwock, D.C. Dey, T.L. Keyser, and D.R. Larsen. 2014. Modeling and mapping oak advance reproduction density using soil and site variables. *Forest Science* 60: 1107–1117. https://doi.org/10.5849/forsci.13-006.

Keyser, T.L. 2019. Resprouting by seedlings of four North American deciduous broadleaved tree species following experimental burning. *Oecologia* 190: 207–218. https://doi.org/10.1007/s00442-019-04397-x.

Kruskal, J.B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29: 1–27. https://doi.org/10.1007/BF02289565.

Lemmon, P.E. 1957. A new instrument for measuring forest overstory density. *Journal of Forestry* 55: 667–668.

Lindbladh, M., and D.R. Foster. 2010. Dynamics of long-lived foundation species: The history of *Quercus* in southern Scandinavia. *Journal of Ecology* 98: 1330–1345. https://doi.org/10.1111/j.1365-2745.2010.01733.x.

Loftis, D.L. 1990. Predicting post-harvest performance of advance red oak reproduction in the southern Appalachians. *Forest Science* 36: 908–916. https://doi.org/10.1093/forestscience/36.4.908.

Lorimer, C.G. 1993. Causes of the oak regeneration problem. In *Oak regeneration: Serious problems practical recommendations.* Ed. by D.L. Loftis and C.E. McGee, 14–39. Gen. Tech. Rep. SE-84. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station. https://doi.org/10.2737/SE-GTR-84.

Lutes, D.C., and R.E. Keane. 2006. *FIREMON: Fire effects monitoring and inventory system*, 410. Fort Collins, CO, USA: Createspace Independent Publishing. https://doi.org/10.2737/RMRS-GTR-164

McCune, B., and J.B. Grace. 2002. *Analysis of ecological communities*. Gleneden Beach, OR: MjM Software Design.

McLean, E.O. 1982. Soil pH and lime requirement. In *Methods of soil analysis: Part 2 chemical and microbiological properties, agronomy monographs,* ed. A.L. 199–24. Madison, WI: American Society of Agronomy and Soil Science Society of America. https://doi.org/10.2134/agronmonogr9.2.2ed.c12.

McNab, H.W. 1989. Terrain shape index: Quantifying effect of minor landforms on tree height. *Forest Science* 35: 91–104. https://doi.org/10.1093/forestscience/35.1.91.

Mehlich, A. 1984. Mehlich 3 soil test extractant: A modification of Mehlich 2 extractant. *Communications in Soil Science and Plant Analysis* 15: 1409–1416. https://doi.org/10.1080/00103628409367568.

Nowacki, G.J., and M.D. Abrams. 2008. The demise of fire and "mesophication" of forests in the eastern United States. *BioScience* 58: 123–138. https://doi.org/10.1641/B580207.

Oksanen, J., F.G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R.B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens, E. Szoecs, and H. Wagner. 2019. vegan: Community ecology package. https://github.com/vegandevs/vegan.

Olson, M.G., A.P. Stevenson, B.O. Knapp, J.M. Kabrick, R.G. Jensen. 2014. Is there evidence of mesophication of oak forests in the Missouri Ozarks? In *Proc. Of the 19th Central Hardwood Forest Conf,* ed. J.W. Groninger, E.J. Holzmueller, C.K. Nielsen, and D.C. Dey, 139–153. General Technical Report NRS-P142. Newtown Square, PA: USDA Forest Service, Northern Research Station. https://research.fs.usda.gov/treesearch/47400.

Palus, J.D., P.C. Goebel, D.M. Hix, and S.N. Matthews. 2018. Structural and compositional shifts in forests undergoing mesophication in the Wayne National Forest, southeastern Ohio. *Forest Ecology and Management* 430: 413–420. https://doi.org/10.1016/j.foreco.2018.08.030.

Parker, G.R., C.M. Ruffner. 2004. Current and historical forest conditions and disturbance regimes in the Hoosier–Shawnee ecological assessment area. In *The Hoosier–Shawnee Ecological Assessment,* ed. F.R. Thompson, 23–49. St. Paul, MN: USDA Forest Service General Technical Report NC-244. https://research.fs.usda.gov/treesearch/12413.

Quackenbush, R.W.E. 2016. An assessment of the competitive ability of oak species in the Central Hardwood Region using both pre-harvest treatment data and stem analysis techniques. West Lafayette, IN: MS Thesis, Purdue University.

R Core Team. 2020. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rawat, B., J.M. Rawat, S. Purohit, G. Singh, P.K. Sharma, A. Chandra, J.P. Shabaaz Begum, D. Venugopal, M. Jaremko, and K.A. Qureshi. 2022. A comprehensive review of *Quercus semecarpifolia* Sm.: An ecologically and commercially important Himalayan tree. *Frontiers in Ecology and Evolution* 10: 1–18. https://doi.org/10.3389/fevo.2022.961345.

Ross, D.S., Q. Ketterings. 1995. Recommended methods for determining soil cation exchange capacity. In *Recommended Soil Testing Procedures for the Northeastern United States*, *Second Edition.* Cooperative Bulletin No. 493. ed. J.T. Sims and A. Wolf, 62-69. Newark, DE: University of Delaware Press.

Sander, I.L., P.S. Johnson, R.F. Watt. 1976. *A guide for evaluating the adequacy of oak advance reproduction.* Gen. Tech. Rep. NC-23, Minneapolis, MN: USDA Forest Service, North Central Research Station. https://research.fs.usda.gov/treesearch/10088.

Schlesinger, R.C., I.L. Sander, and K.R. Davidson. 1993. Oak regeneration potential increased by shelterwood treatments. *Northern Journal of Applied Forestry* 10: 149–153. https://doi.org/10.1093/njaf/10.4.149.

Schulte, E.E., and B.G. Hopkins. 1996. Estimation of soil organic matter by weight loss-on ignition. In *Soil organic matter: Analysis and interpretation.* SSSA Special Publications. ed. F.R. Magdoff, M.A. Tabatabai, and E.A. Hanlon, 21–31. Madison, WI: Soil Science Society of America. https://doi.org/10.2136/sssaspecpub46.c3.

Soil Survey Staff, Natural Resources Conservation Service, USDA. 2023. *Web soil survey* http://websoilsurvey.nrcs.usda.gov/. Accessed August 10, 2023.

Swaim, J.T., D.C. Dey, M.R. Saunders, D.R. Weigel, C.D. Thornton, J.M. Kabrick, and M.A. Jenkins. 2018. Overstory species response to clearcut harvest across environmental gradients in hardwood forests. *Forest Ecology and Management* 428: 66–80. https://doi.org/10.1016/j.foreco.2018.06.028.

Turman Creek Tree Farms. 2013. *Work plan for 66 TSI-chem treat task order 2013–4*. Tell City, IN: Hoosier National Forest.

USDA, NRCS. 2022. *The PLANTS database [WWW Document]*. Greensboro, NC: National Plant Data Team. https://plants.usda.gov/. Accessed 3.23.22.

Van Kley, J.E., G.R. Parker, D.P. Franzmeier, and J.C. Randolph. 1995. *Field guide: Ecological classification of the Hoosier National Forest and surrounding areas of Indiana*. Bedford, IN: USDA Forest Service, Hoosier National Forest.

Vander Yacht, A.L., K.D. Keyser, S.A. Barrioz, C. Kwit, M.C. Stambaugh, W.K. Clatterbuck, and D.M. Simon. 2019. Reversing mesophication effects on understory woody vegetation in mid-southern oak forests. *Forest Science* 65: 289–303. https://doi.org/10.1093/forsci/fxy053.

Varner, J.M., J.M. Kane, J.K. Hiers, J.K. Kreye, and J.W. Veldman. 2016. Suites of fire-adapted traits of oaks in the southeastern USA: Multiple strategies for persistence. *Fire Ecology* 12: 48–64. https://doi.org/10.4996/fireecology.1202048.

Venables, W.N., and B.D. Ripley. 2002. *Modern applied statistics with S*, 4th ed. New York: Springer.

Woodall, C.W., J.A. Perez, T.R. Thake. 2007. *Forest resources of the Hoosier National Forest, 2005. NRS-RB-18*. Newtown Square, PA: USDA Forest Service, Northern Research Station. https://doi.org/10.2737/NRS-RB-18.

Authors and Affiliations

Sarah J. Rademacher[1,2] · Daniel C. Dey[3] · John M. Kabrick[3] · Robert W. E. Quackenbush[1,4] · Michael R. Saunders[1] · J. Travis Swaim[5] · Christopher D. Thornton[5] · Michael A. Jenkins[1]

✉ Michael A. Jenkins
jenkinma@purdue.edu

Sarah J. Rademacher
s.jean.rade@gmail.com

Daniel C. Dey
daniel.c.dey@usda.gov

John M. Kabrick
john.kabrick@usda.gov

Robert W. E. Quackenbush
rwquacke@gmail.com

Michael R. Saunders
msaunder@purdue.edu

J. Travis Swaim
justin.swaim@usda.gov

Christopher D. Thornton
christopher.thornton@usda.gov

1 Department of Forestry and Natural Resources, Purdue University and the Hardwood Tree Improvement and Regeneration Center, 715 Mitch Daniels Boulevard, West Lafayette, IN 47907, USA

2 University of Minnesota Landscape Arboretum, 3675 Arboretum Drive, Chaska, MN 55318, USA

3 Northern Research Station, USDA Forest Service, 202 ABNR Building, Columbia, MO 65211, USA

4 Walnut Ridge Field Service Center, Natural Resource Conservation Service, 1100 West Main Street, Walnut Ridge, AR 72476, USA

5 Hoosier National Forest, 811 Constitution Avenue, Bedford, IN 47421, USA