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Evaluating the impact of prescribed surface fire on seedlings in the Central Hardwood Region, USA

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Oak (*Quercus*) is being successionally replaced by maple (*Acer*) across much of the eastern deciduous forest. Past research on the close relationship between oak and fire has led forest managers to use prescribed surface fires to deter this replacement. However, there has not been a comprehensive evaluation of the effectiveness of prescribed fire by managers, particularly in the Central Hardwood Region. For example, it is not known how many repeat applications of prescribed fire are needed to accumulate enough oak reproduction to successfully re-establish oak-dominated stands. Tree reproduction and midstory composition were systematically surveyed across 63 mature, oak-dominated stands ranging in prescribed fire histories and aspects on the Hoosier and Wayne National Forests in southern Indiana and Ohio, respectively. These stands represent the vast majority of stands burned to promote oak regeneration since 1990 in these two National Forests. Across all sites, seedlings in the white oak group (section *Quercus*) and red oak group (section *Lobatae*) comprised 47.8 ± 3.3 per cent and 8.2 ± 1.6 per cent (mean ± SE), respectively, of all seedlings. In comparison, common competing species (maples and American beech) comprised 5.4 ± 1.4 per cent of all seedlings. Mid- and overstory basal area, percent slope, years since last burn, and total number of burns significantly affected oak seedling density. Greater increases in taller, competitive oak seedling density occurred after sites had been burned three times and with high frequency (≤4 years between burns). However, results also suggest that if an established midstory already exists or fire has not been used on the landscape for almost a decade, repeat applications of prescribed fire will not likely increase oak regeneration in the short term without concurrent treatment of midstory stems.

Introduction

Oaks (*Quercus* spp.), a group of foundational species in many eastern North American forest ecosystems, are slowly being successionally replaced by maples (*Acer* spp.) and other mesic species throughout their range. There are a number of reasons for this replacement including historic and current oak decline due to drought (Walters and Munson, 1980), *Armillaria* infection (Brazee and Wick, 2009), insect defoliation events (Trefry, 1984), deer herbivory (Oswalt *et al.,* 2006) and natural senescence. These factors lead to oak mortality, an increase in the number and size of canopy gaps, and eventually the proliferation of shade-tolerant species poised to reach maturity after gap creation. This successional shift is a self-reinforcing process, termed mesophication (Nowacki and Abrams, 2008), that fundamentally shifts the disturbance regimes of these oak-dominated forests from fire-mediated (shade-intolerant oak) to self-replacing (shade-tolerant maple). Correspondingly, this regime shift and compositional change alters the ecosystem services that are provided. There are 96 known species of forest-dwelling birds and mammals that consume acorns, a critical energy source during the dormant season for many vertebrate species (Martin *et al.,* 1961). Therefore, mesophication will undoubtedly change wildlife communities as mast availability declines and other habitat requirements are altered.

Changes will also cascade to forest floor communities through a self-reinforcing process. Maple litter contains less lignin than oaks and compresses into dense layers easily after leaf fall. Moisture becomes easily trapped in the litter and aeration is minimized, increasing the speed of decomposition and altering soil formation dynamics (Palus *et al.,* 2018). Trapped forest floor moisture coupled with a dense, packed litter alters the fuel dynamics to such an extent that surface fires become exceedingly rare and largely ineffective to affect regeneration dynamics, even when prescribed (Varner *et al.,* 2021). Therefore, through mesophication, maples and other mesic species are creating an ever-increasing shady, mesic environment in which these shade-tolerant species outcompete mid-tolerant oak seedlings, grow into the midstory and eventually self-replace (Abrams and Nowacki, 1992; Abrams, 2005; Nowacki and Abrams, 2008).

Prescribed fire has been increasingly used by land managers in the past few decades to facilitate oak regeneration and break the cycle of mesophication, but with varying results (McLauchlan *et al.,* 2020). Managers are attempting, in effect, to mimic pre-settlement disturbance regimes that produced the oak-dominated forests of the past but have since been altered due to early 20th century fire suppression policies (Crow, 1988; Lorimer, 1993; Crow *et al.,* 1994; Aldrich *et al.,* 2005). However, there seems to be no common fire prescription that consistently establishes oak reproduction on all sites; in fact, there are reports of positive, negative and neutral results from use of prescribed fire over the past few decades (Brose *et al.,* 2014). A single application of prescribed fire can provide either negative or negligible outcomes for oak seedlings depending on context and site conditions (Loftis, 1990; Collins and Carson, 2003; Dolan and Parker, 2004; Albrecht and McCarthy, 2006; Arthur *et al.,* 2015); dual applications provide mixed responses as well (Merritt and Pope, 1991; Arthur *et al.,* 1998; Schuler *et al.,* 2013). Furthermore, Arthur *et al.* (1998) demonstrated that using only one burn may create more favourable conditions for less fire-resistant species like maple, shrubs and herbaceous species. By topkilling part of the midstory canopy, quick-growing maple can infill the holes, creating even shadier conditions for any resulting oak regeneration (Brose *et al.,* 2005).

Studies monitoring long-term effects of multiple applications of fire ($\geq$3) are rare, but generally describe positive benefits to oak regeneration (Huddle and Pallardy, 1996; Stratton, 2007). This is particularly true when prescribed fire is used on more xeric sites; oaks are better adapted to these drier environments than other species, so oak seedlings may be recruited on these sites with more success than on mesic sites where conditions favour other moisture-loving species (Hodges and Gardiner, 1993; Lorimer, 1993). However, if fire is used too frequently, mortality of oak species can greatly increase as the incessant disturbance depletes the carbohydrate reserves of young oak seedlings and they perish alongside their competitors (Dey and Hartman, 2004).

Past research has also suggested that the interval between multiple prescribed fires is extremely important. At a Tennessee site, Stratton (2007) reported that even a 5-year fire return interval was too short a time span to allow successful oak reproduction time to grow to a fire-resistant size. Historically, the pre-settlement surface fire return interval in the Central Hardwood Region (CHR) is believed to have averaged ~13 years, but later in the 1800s this average decreased to 7 years as industry and accidental fires increased in the region (Brose *et al.,* 2014). This historic return interval may appear to provide strong guidance for a return interval between modern prescribed fires; however, many oak forests fundamentally changed in structure, originally consisting of an open understory to one of dense under- and midstory layers, and in composition, originally from oak-hickory dominance to a diffuse mixture of oak with increasing maple and beech components. While undocumented oak regeneration issues may have historically occurred, most eastern North American oak forests certainly cannot currently be described as they were upon European settlement (Greeley and Ashe, 1907).

Mesophication creates a positive feedback loop that prescribed fire alone may not mitigate, and the scientific community has yet to reach a consensus on whether forest management plans utilizing prescribed burns will be successful to restore oak forests (Matlack, 2013; Stambaugh *et al.,* 2015). While several research studies have demonstrated the advantages of using prescribed fire, it remains unclear if, in practice, fire practioners are getting desired oak regeneration results, and if adjustments should be made to fire prescriptions. Documenting the effects of prescribed surface fire set by land managers and fire practioneers, but outside the strict controls of stand-level experimental studies where researchers closely regulate fire weather and fuel parameters, is necessary to obtain better estimates of the realized ecological benefits and economical costs of prescribed fire as applied across the landscape (Stanis *et al.,* 2019; Mann *et al.,* 2020).

The main objective of this study is to retrospectively examine if and to what extent managers' applications of prescribed fire have met the goal of promoting oak regeneration. We focused this study on the Hoosier and Wayne National Forests in southern Indiana and Ohio, respectively. These forests have significant oak-dominated forest acreages that include much more mesic site conditions than in many parts of the range of eastern oaks. We inventoried seedling and mid-/overstory data from 63 sites that differed in prescribed fire history, ranging from controls with similar management and composition, but no use of prescribed fire, to sites with six prescribed fires since 1990. The burnt sites surveyed represent a majority of oak-dominated stands receiving prescribed fire in these two National Forests. More specifically, our study objectives were to: (1) analyze how the density of competitive oak reproduction, defined as seedlings over 30 cm tall, compared to the density of mesic species (maple and beech) with an increasing number of prescribed fires; (2) determine how seedling species composition changed as the time lag since the last prescribed burn increased and (3) investigate how topographic and stand structural variables were mediating prescribed fire effects on oak seedling density and composition.

Methods

Study sites

This study was conducted in the Hoosier National Forest (HNF) in southern Indiana and the Wayne National Forest in southern Ohio (WNF). The HNF comprises over 80 000 hectares of the unglaciated portions of southern Indiana; specifically, the Shawnee Hills and Highland Rim Natural Regions (Homoya *et al.,* 1985; Woodall *et al.,* 2007). The area mainly consists of a sandstone-shale bedrock, with several deep stream valleys and wooded hillsides to the east, and stony outcrops of rock bluffs with more arable land to the west (Ponder Jr., 2004). Sandstone-derived soils, like Crider silt loam and the Wellston-Zanesville-Berks Association are most common (Homoya *et al.,* 1985). Sinkholes produced by the breakdown of limestone bedrock are also an important geologic feature of the region. Average yearly precipitation is 1120–1370 mm and the average temperature is between 13 and 16°C across the HNF (Ponder Jr., 2004).

Prior to European settlement the HNF was mainly deciduous, dominated by oak (*Quercus*), hickory (*Carya*), beech (*Fagus*) and aspen (*Populus*) (Ponder Jr., 2004). The forest was heavily cutover in the 1800s and early 1900s prior to the establishment of the HNF in 1935. Common second-growth overstory species today include white oak (*Quercus alba*), northern red oak (*Quercus rubra*), shagbark hickory (*Carya ovata*), and pignut hickory (*Carya glabra*) in the upland forests and sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) on more mesic sites (Homoya *et al.,* 1985). Fire, either through natural ignitions or deliberately set by Native Americans, can be assumed to have been a part of this landscape for centuries, according to the written observations of the first European settlers to the region (Homoya *et al.,* 1985; Jenkins, 2013). These settlers described open and park-like forests, similar to most eastern hardwood forests, without much understory or midstory present (Greeley and Ashe, 1907). In more recent years, however, prescribed fire has been used to promote oak and hickory regeneration, reduce fuel loads, and restore barren habitats (Stanis *et al.,* 2019; Mann *et al.,* 2020).

The ~100 000 ha WNF is located in the unglaciated Allegheny Plateau in southern Ohio (Palus *et al.,* 2018). Its topography consists of high hills, sharp ridges, and narrow valleys and the bedrock is comprised mostly of sandstone, siltstone and shale, while the soils are acidic, well-drained loams or silt loams (Sutherland *et al.,* 2003). Due to the lack of mineral inputs from the limestone bedrock commonly found in the HNF, Gilpin and/or Steinsburg series complexes or associations dominate this region (Boerner and Sutherland, 2003). Average yearly precipitation is between 810 and 960 mm and annual temperatures range from around 10 to 13°C (Palus *et al.,* 2018).

Similar to the HNF, this oak-dominated forest was also described as open and park-like before European settlement. Even after the arrival of settlers, but before fire suppression policies, the fire return interval was between 5 and 15 years (Sutherland *et al.,* 2003). After settlement, the forests were harvested for the charcoal iron industry; most forests have been undergoing secondary succession since the decline of that industry in the early 1900s. Currently, the sapling layer is dominated by shade tolerant species like red and sugar maple, blackgum (*Nyssa sylvatica*) and beech (Hutchinson *et al.,* 2003). The most abundant overstory species include white, chestnut (*Quercus montana*), and black (*Quercus velutina*) oak, various hickories, and red (*Acer rubrum*) and sugar maple. Overstory white oak, especially in size classes under 30 cm, are less abundant on moist sites and sugar maple of all sizes are rare on dry sites (Yaussy *et al.,* 2003). As in the HNF, prescribed burns are currently used by managers to promote oak regeneration in the understory. Burns in both national forests are usually low-intensity and patchy, producing a heterogeneous landscape without large swaths of complete litter consumption and mineral soil exposure.

Plot selection

From stands previously inventoried for prescribed fire damage to overstory timber (Stanis *et al.,* 2019; Mann *et al.,* 2020), we selected 47 stands that had prescribed fire history and 16 unburnt control stands across the two national forests. All stands were dominated (>50 per cent basal area; BA) by oak and hickory species. Each had merchantable timber with an average diameter at breast height (DBH) of at least 25 cm. Each stand had a relatively homogeneous species composition, aspect and age structure, and was usually between 4 and 13 ha (Stanis *et al.,* 2019, Mann *et al.,* 2020). Stands were further classified using burn class, the number of prescribed burns that the stand had received since 1990, and by predominant aspect. Aspect, in particular, has repeatedly been shown to influence the intensity of prescribed burns, with slopes on south- and west-facing aspects usually hosting more intense fires than their wetter counterparts on easterly or northerly aspects (Pyne *et al.,* 1996; Estes *et al.,* 2017). Management records of pre-treatment conditions do not exist, as stands were often part of larger landscape-scale burns (often exceeding 100 ha) and managers rarely had the resources to adequately monitor stands before and after such prescriptions. Appendices in Mann (2019) and Stanis (2018) comprise the most complete stand-level data available.

Each stand was sampled with 15 points, using the same locations as Stanis *et al.* (2019) and Mann *et al.* (2020). Their point selection procedures used the fishnet or point ArcGIS tool to randomly select points until at least 8 points were on slopes with aspects corresponding to the predominant stand aspect (8/15 points on north-facing slopes for a stand with a northerly aspect). Points had to be at least 30 m away from each other in order to avoid double-sampling of overstory trees. Although care was taken to represent as many total burn numbers and years since the last burn as possible, weather and personnel ultimately dictate when burns can happen, resulting in an unbalanced design. For example, the three-burn category contained 19 stands while the two-burn category contained 5, and 20 stands were burned 1 year prior to sampling but the 2-, 7- and 10-year categories each contained only one stand (see Table S-2). One could argue that an unbalanced study design could weaken our statistical inference and, instead, that we should have selected a subset of stands to achieve a more balanced design. However, we felt given the high variability often seen in regeneration responses, coupled with the heterogeneous nature of prescribed surface fire intensities observed within the CHR, it was more prudent to include all available sites in order to increase sample size.

Data collection

Field sampling methods were loosely based on the SILVAH protocol for collecting data on oak regeneration in the Allegheny Mountain region (Brose *et al.,* 2008). We measured aspect and percent slope at the centre of each sample point. One midstory plot, three reduced-midstory subplots and three regeneration subplots were installed at each point. The midstory plot captured all potential sources of interference to successful regeneration by quantifying both midstory trees (DBH between 10 and 25 cm) and groundcover; the reduced-midstory plots just captured sources of interference in the form of midstory trees.

The 3.8 m^2 regeneration subplots were placed with their centers 3.5 m from the plot centre, 120° away from each other (i.e. one subplot 3.5 m from plot centre at 0° azimuth, one subplot at 120° and another subplot at 240°). Within each regeneration subplot, we measured all woody stems greater than 15 cm tall with a DBH less than 10 cm. We recorded species, height to the nearest cm and root collar diameter (RCD) to the nearest 5 mm for each individual.

The three reduced-midstory subplots, 10.2 m^2 each, were overlain on each regeneration subplot. We quantified midstory trees in these subplots, measuring the species, DBH, and which regeneration subplot (0°, 120°, or 240°) the midstory was associated with for each species with a DBH between 10 and 25 cm.

The 201 m^2 midstory plot was also centred on the sample plot centre, completely engulfing both the reduced-midstory and regeneration subplots. We quantified all midstory trees and

Table 1 Summary of all seedling (height > 15 cm, DBH < 10 cm) species found across all plots

Common name	Latin name	Count
White oak	*Quercus alba*	6289
Sassafras	*Sassafras albidum*	1841
Hickory spp.	*Carya*	1203
Black oak	*Quercus velutina*	857
Northern red oak	*Quercus rubra*	649
Eastern redbud	*Cercis canadensis*	574
Tulip poplar	*Liriodendron tulipifera*	500
Chestnut oak	*Quercus montana*	495
American elm	*Ulmus americana*	426
Sugar maple	*Acer saccharum*	301
American beech	*Fagus grandifolia*	281
Red maple	*Acer rubrum*	135
Ironwood	*Ostrya virginiana*	141
Blackgum	*Nyssa sylvatica*	128
Pawpaw	*Asimina triloba*	79
Black cherry	*Prunus serotina*	75
Red pine	*Pinus resinosa*	56
Slippery elm	*Ulmus rubra*	54
Flowering dogwood	*Cornus florida*	28
Blackjack oak	*Quercus marilandica*	25
Sweetgum	*Liquidambar styraciflua*	12
Bur oak	*Quercus macrocarpa*	11
Other spp.[1]		40

[1]Other species include: *Diospyros virginiana* (7), *Fraxinus americana* (7), *Q. imbricaria* (6), *Celtis occidentalis* (3), *Aesculus glabra* (3), *Tilia cordata* (3), *Q. muehlenbergii* (2), *Oxydendrum arboreum* (2), *Juniperus virginiana* (2), *T. americana* (1), *Platanus occidentalis* (1), *Carpinus caroliniana* (1), *Q. stellata* (1), *Malus ioensis* (1).

groundcover within this plot. We recorded the species and DBH of each midstory tree and the percent cover, to the nearest 5 per cent, for each taxa group comprising the groundcover of the entire midstory plot (i.e. briar/thorny shrubs, shrubs, forbs, grasses, herbaceous vegetation, moss, sedges, tree seedlings and rocks/bare ground).

Data preparation

Total midstory basal area (BA), oak midstory BA (oak BA) and mesic species midstory BA (mesic BA) were each calculated for each stand. Oak BA was defined as total midstory BA of all oak species found on the study sites: white, chestnut, northern red, black, bur (*Quercus macrocarpa*), chinkapin (*Quercus muehlenbergii*), post (*Quercus stellata*), blackjack (*Quercus marilandica*) and shingle (*Quercus imbricaria*). Mesic BA was defined as the midstory BA of the shade-tolerant species most likely to interfere with the growth and/or survival of oak reproduction: American beech, sugar maple and red maple. Overstory BA, trees per acre and site index were estimated based on Stanis *et al.* (2019).

Site index, trees per acre and percent slope were classified into 'low', 'medium' and 'high' categories based on the first quartile, median and third quartile of their respective distributions, as the absolute values associated with these variables for any given plot were far less important than their values relative to all other plots in the study. The observed ranges for all stand structural and environmental variables can be found in Appendix A. Aspect was also reduced into north (north and east aspects) and south (south and west aspects) based on the stand classification system of Stanis *et al.* (2019).

Due to the highly unbalanced design, stands were aggregated into year classes that corresponded to the time since burn; these were: 1 year, 2–3 years, 4–7 years and 8–10 years. These classes captured immediate, short-, medium- and long-term regeneration lags to fire disturbance. Results for unaggregated data can be found in the online supplementary materials.

The likelihood of survival for short seedlings is inherently low (Brose *et al.*, 2008), so we completed the statistical analyses using only the seedlings that were ≥30 cm in height; descriptive data summaries include all seedlings. We summarized seedling density (seedlings per hectare) per sub-plot, then aggregated the data to the plot-level so local environmental variables like slope and aspect could be used as predictors without averaging across an entire stand.

Statistical analysis

To test the effect of repeated burns (Objective 1) and time since last burn (Objective 2) on seedling density, we used one-way analysis of variance (ANOVA) and post-hoc Tukey's Honest Significant Difference multiple comparison test (hereafter, Tukey HSD) with burn number and year class as treatments, respectively. These analyses were conducted using densities of all competitive seedlings, of competitive oak seedlings, and of competitive mesic seedlings (maple and beech) for both Objective 1 and Objective 2. For each test, we further screened for normality using the Shapiro–Wilk test (Shapiro and Wilk, 1965); Appendix A shows these results for oak seedling densities among burn classes and years since last burn classes.

The effects of topographic and structural variables on the relationship between prescribed fire and regeneration (Objective 3) were tested two ways. First, we used random forests (Breiman, 2001) to predict oak seedling densities as a function of stand characteristics, environment and burn variables. Number of burns, years since the last burn class, aspect, slope, trees per acre, site index, overstory BA, midstory BA, oak BA and mesic BA were included to predict densities of all oak species seedlings. Regression trees are widely used in ecology due to their ease of use, high accuracy and success with classifying complex relationships among many variables (Cutler *et al.*, 2007). Random forest is a nearly nonparametric bagged regression tree approach; the only two defined parameters are the number of variables at each node and the total number of 'trees' in the forest (Liaw and Weiner, 2002). Relative importance of each variable in a random forest model is calculated via a measurement of increase in node purity and mean square error (MSE), with higher values of each metric indicating more importance. Because these two metrics may be biased depending on analysis and experimental design (Strobl *et al.*, 2007; Archer and Kimes, 2008), from those variables which deemed important by both node purity and reduction in MSE, we used one-way ANOVA and Tukey HSD to more specifically investigate the variables' impacts

Table 2 Summary statistics categorized by burn number

Burn count	Stands	Seedlings ha^{-1}	% Tall	% White oak	% Red oak	% Maple/beech
0	16	10 500 ± 25	53.8	55.1	9.3	11.3
1	10	9930 ± 40	45.6	38.2	4.0	6.0
2	5	10 300 ± 53	63.4	42.8	13.7	4.3
3	19	12 100 ± 30	60.4	40.7	11.7	3.1
4	6	14 000 ± 50	57.4	55.4	10.6	3.9
6	7	21 100 ± 57	72.1	54.9	14.8	1.2

Stands = number of stands that have been burned that many times; seedlings ha^{-1} = the number of seedlings per ha for that burn count ± SEM; % tall = percentage of total seedlings that are above 30 cm in height; % white oak = percentage of total seedlings that belong to the white oak species group; % red oak = percentage of total seedlings that belong to the red oak species group; % maple/beech = percentage of total seedlings that are either sugar maple, red maple or American beech.

on oak seedling density within different burn numbers and year classes.

All analyses used R 3.6.1 (R core team, 2019) and the 'randomForest' package (Liaw and Weiner, 2002). Significance was determined at $\alpha = 0.05$.

Results

A total of 14 200 seedlings were measured across the 63 stands. White oak, black oak, chestnut oak and northern red oak were among the most prevalent oak seedlings counted (Table 1). Sassafras (*Sassafras albidum*), hickory species, eastern redbud (*Cercis canadensis*), American beech and tulip poplar seedlings were the next most prevalent species encountered. Sugar and red maple seedlings were both found on plots, but at low densities.

Effect of repeat burns on regeneration

Stands that were burned six times had the highest overall seedling density (21 100 ± 57 seedlings ha^{-1}) (mean ± SE) and stands burned only once had the lowest seedling density (9930 ± 40 seedlings ha^{-1}) (Table 2). Burn number, i.e. the number of burns a stand received since 1990, significantly affected overall seedling density ($F_{5,\,8401} = 351$, $P < 0.001$). Control plots had fewer seedlings than plots burned at least three times ($P < 0.001$ for all). Plots burned once had fewer seedlings than plots burned three ($P = 0.025$), four ($P < 0.001$) and six ($P < 0.001$) times, plots burned twice had a lower seedling density than plots burned four ($P = 0.025$) and six ($P < 0.001$) times, and plots burned six times had a higher density of seedlings than plots burned three and four times ($P < 0.001$ for both).

Oak seedling density was also significantly affected by burn number ($F_{5,\,4768} = 327$, $P < 0.001$). Control plots had a higher oak seedling density than plots burned once ($P = 0.037$), but lower density than plots burned four ($P < 0.001$) and six ($P < 0.001$) times. Plots burned once had a lower oak seedling density than plots burned at least three times ($P < 0.001$ for all), plots burned three times had fewer oak seedlings than plots burned four and six times ($P < 0.001$), and plots burned six times also had a higher density than plots burned two and four times ($P < 0.001$ for all).

The seedling density of mesic species was significantly impacted by burn number ($F_{5,\,452} = 5.55$, $P < 0.001$). Control plots had a higher mesic seedling density than plots burned one ($P < 0.001$) and three times ($P = 0.014$). No other burn numbers differed significantly.

The white oak group (white, chestnut, bur, chinkapin, and post oak) comprised a majority of seedlings in stands burned four times (55.4 per cent of all seedlings) and six times (54.9 per cent), but was also very common in stands without burns (55.1 per cent) (Table 2, Figure 1). Seedlings in the red oak group (northern red, black, blackjack, and shingle oak) comprised the largest proportion in stands with two (13.7 per cent of all seedlings) and six (14.8 per cent) burns, but any burned stand had at least 10 per cent red oak seedlings (Table 2, Figure 1). Mesic species seedlings (American beech, red maple, sugar maple) made up less of the total seedling population as the burn number increased, declining from 11.3 per cent of all seedlings in unburned stands to 1.2 per cent of all seedlings in stands burned 6 times (Table 2, Figure 1).

Stands burned six times had the highest proportion of seedlings over 30 cm tall (72.1 per cent of all seedlings) and those burned once had lowest proportion (45.6 per cent of all seedlings) (Table 2). Generally, as the number of burns increased, so did seedling density and proportion of seedlings over 30 cm tall (Figure 2).

Effect of time since last burn on regeneration

Overall seedling density generally declined for several years after a burn, but started to rebound in the 8th year (Figure 3). Stands burned 1 year prior had the highest seedling density (14 700 ± 30 seedlings ha^{-1}) and stands burned 4–7 years before sampling had the lowest (5880 ± 61 seedlings ha^{-1}) (Table 3).

Years since burn significantly affected, overall ($F_{4,\,8402} = 220.6$, $P < 0.001$), oak ($F_{4,\,4769} = 184.4$, $P < 0.001$) and mesic ($F_{4,\,453} = 6.12$, $P < 0.001$) seedling density. The density of all seedling species on unburned plots was lower than plots burned within the last 3 years ($P < 0.001$ for all). The 1 year post-burn category was significantly higher than all other categories ($P < 0.001$ for all). The 2–3 years post-burn category was also higher than 4–7 years and 8–10 years ($P < 0.001$ for both). The 4–7 and 8–10 categories did not differ in seedling density response. Oak seedling densities on control plots were lower than plots burned one ($P < 0.001$) and 2–3 ($P = 0.005$) years prior. The 1 year post-burn category was higher than all other categories ($P < 0.001$ for all). Additionally, the 2–3 year category was higher than the

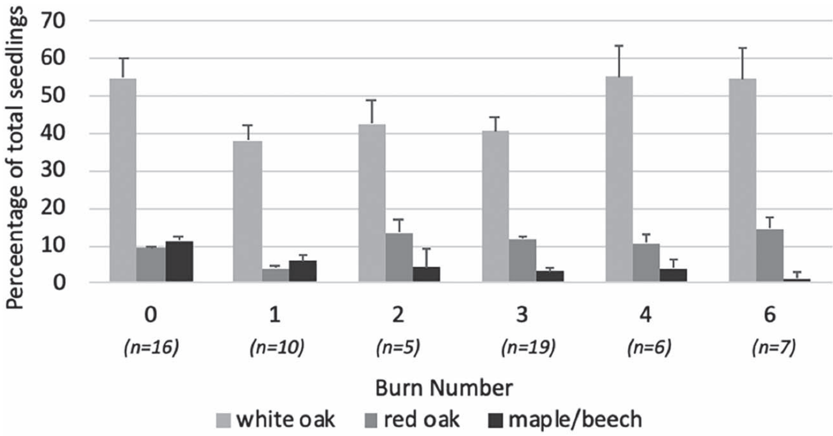

Figure 1 Percentage of total seedlings that belong to either the white oak group, red oak group or maple/beech group. Stand sample sizes for each burn class are shown in italics below the *x*-axis, and error bars are displaying the standard error of the mean.

Table 3 Summary statistics categorized by time since the last burn classes

Years since last burn	Stands	Seedlings ha^{-1}	% Tall	% White oak	% Red oak	% Maple/beech
1	20	14 700 ± 30	63.7	47.3	15.3	2.4
2–3	10	13 000 ± 75	72.4	52.4	9.3	1.8
4–7	6	5880 ± 61	44.1	45.2	4.3	12.8
8–10	11	11 810 ± 103	51.2	34.0	10.4	8.2

Stands = number of stands that have been burned that number of years ago; seedlings ha^{-1} = the number of seedlings per ha for that year count ± SEM; % tall = percentage of total seedlings that are above 30 cm in height; % white oak = percentage of total seedlings that belong to the white oak species group; % red oak = percentage of total seedlings that belong to the red oak species group; % maple/beech = percentage of total seedlings that are either sugar maple, red maple or American beech.

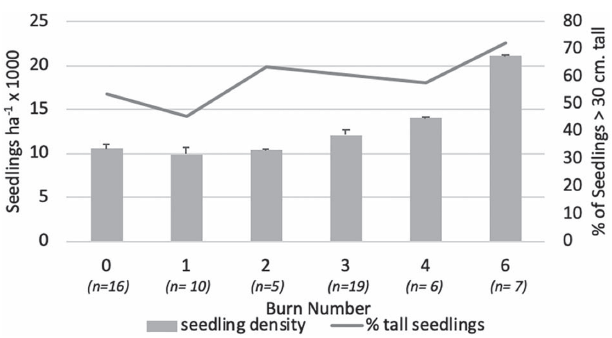

Figure 2 Seedling density (seedlings $ha^{-1} \times 1000$) and percentage of total seedlings that were taller than 30 cm displayed by total number of burns. Stand sample sizes for each burn class are shown in italics below the *x*-axis, and error bars are displaying the standard error of the mean.

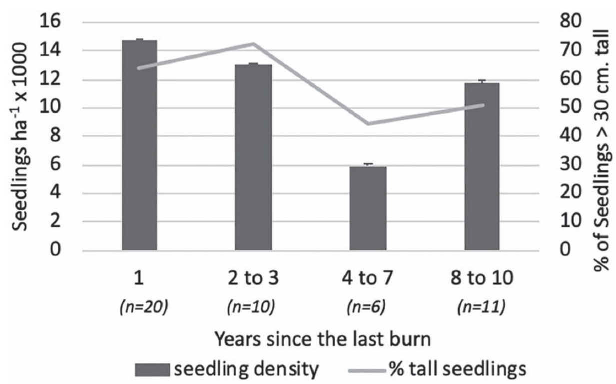

Figure 3 Seedling density (seedlings $ha^{-1} \times 1000$) and percentage of total seedlings taller than 30 cm displayed by the number of years since the last burn category. Stand sample sizes for each year category are shown in italics below the *x*-axis, and error bars are displaying the standard error of the mean.

8–10 category ($P < 0.001$), but no other categories differed. Mesic species seedling density on unburned plots was higher than those burned within the last 3 years ($P < 0.001$ for all). No other year classes differed.

Mesic species seedlings were proportionality lowest in the first 4 years after a burn (1.3–2.4 per cent of all seedlings present), while oak seedling densities were variable but often an order of magnitude or more higher (Table 3). White oak seedlings, in particular, accounted for >30 per cent of the seedling density at all times, while red oak seedlings decreased in proportion for the first 7 years post-burn and then increased thereafter (Figure 4). Likewise, seedlings of all species over 30 cm tall dominated in the first 3 years after a burn (63.7–72.4 per cent of all seedlings; Table 3).

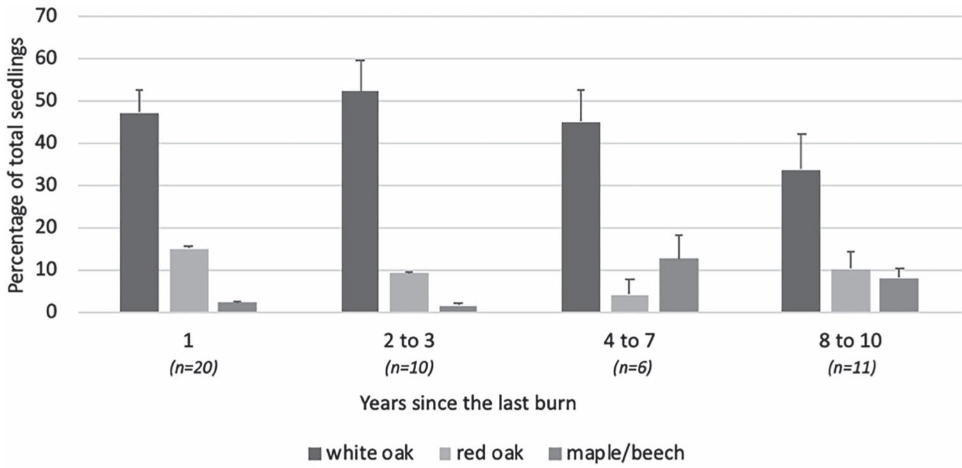

Figure 4 Percentage of total seedlings that belong to either the white oak group, red oak group or maple/beech group displayed by the number of years since the last burn category. Stand sample sizes for each year are shown in italics below the *x*-axis, and error bars are displaying the standard error of the mean.

The seedling density of all species ($F_{10,\,8396} = 184.9$, $P < 0.001$) and oak species ($F_{10,\,4763} = 170.8$, $P < 0.001$) were both significantly affected by the interaction between the number of years since the last burn and total burn number. Mesic species seedling density was not affected by this interaction.

Effect of topography and stand structure on regeneration

In the random forest model the most important variables, which explained 51.1 per cent of the variance, when predicting oak seedling density were mostly a mix of topographic and structural variables: slope, burn number, midstory BA, mesic BA, overstory BA, and oak BA (Figure 5). Trees per acre and years since burn were of moderate importance, and aspect and site index were the least important variables (Figure 5).

All important random forest predictors significantly affected oak seedling density. In addition to burn number, oak seedling density was significantly affected by slope ($F_{2,\,4771} = 26.33$, $P < 0.001$), midstory BA ($F_{106,\,4667} = 30.82$, $P < 0.001$), mesic BA ($F_{1,\,4772} = 100.3$, $P < 0.001$), oak BA ($F_{1,\,4772} = 89.16$, $P < 0.001$) and overstory BA ($F_{1,\,4772} = 8.04$, $P = 0.005$).

All slope categories differed from each other ($P < 0.001$ for all, except $P = 0.05$ when comparing low and high slopes). Oak seedling density was highest in moderately sloped sites, especially as the burn number increased (Figure 6). As midstory BA, mesic BA, oak BA, and overstory BA increased, oak seedling density decreased.

Discussion

Repeated applications of prescribed fire favour oak

Our results suggest that surface fire, as currently prescribed by managers, increases oak regeneration density with repeated applications. Overall seedling density increased with burn number (Figure 1, Table 2), and these results suggest that as long as a site is burned three or more times, overall seedling density will increase. Arthur *et al.* (1998) found that seedling density of oak and competitor species increased after two burns of differing intensities, so it appears that repeat prescribed fires benefit the regeneration layer in general.

Sites burned once had a lower density of oak seedlings than control sites; this negative effect has been observed before (Loftis, 1990; Collins and Carson, 2003; Dolan and Parker, 2004; Albrecht and McCarthy, 2006). A single burn often reduces the density of all seedlings (Dolan and Parker, 2004) and, depending on other stand characteristics, may lead to a recolonization of maple and other interfering species (Albrecht and McCarthy, 2006). Miller *et al.* (2017), for example, found that stands treated with midstory removal or a shelterwood harvest in concert with herbicide application or deer fencing all had better oak seedling regeneration responses than stands burned only once. Our results suggest that, in practice, at least four total burns are needed before a significant positive impact on oak seedling density emerges, with densities remaining high even after six burns.

Mesic species were negatively affected by the number of burns, as also reported elsewhere (Alexander *et al.,* 2008). The regeneration layer never had a large proportion of mesic seedlings (Figure 2, Table 2), and density on control plots exceeded those burned one and three times, suggesting that any number of burns can decrease mesic seedling density. It is important to note, however, that the stands included in this study were not 'average' stands for the CHR, as they were originally selected for inclusion in the prescribed burning program due to their likelihood to be more favourable to oak regeneration. Therefore, average stands would likely have a larger component of non-oak seedling species leading to an even more pronounced negative effect of repeat burns. Additionally, with increasing applications of prescribed fire, mature maples and beech can be injured or killed by fires (Mann *et al.,* 2020), reducing their reproductive capacity and their propagule contribution. For example, maple and beech seedling numbers remained low in the first 4 years following a burn on our sites (Table 3, Figure 4), suggesting both a direct effect through reduced seedling survival and reduced seed production, either through injury or death of mature individuals (Brose *et al.,* 2014).

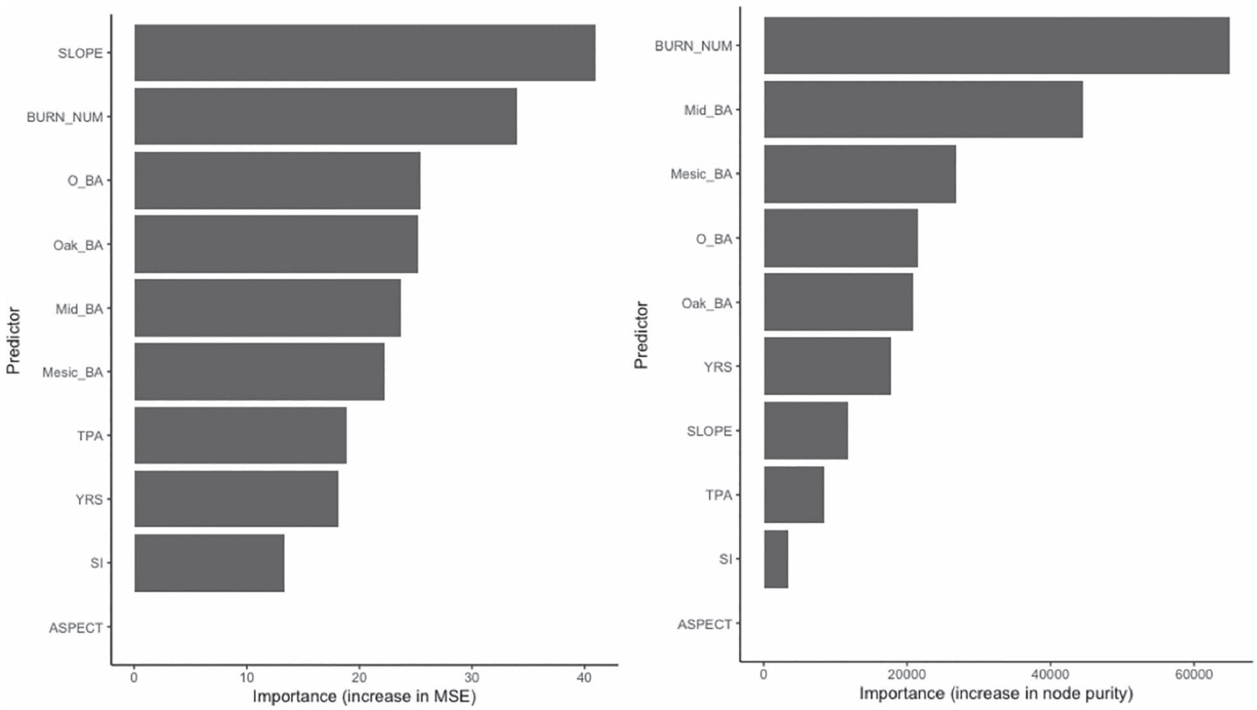

Figure 5 The importance of each predictor variable, measured by the increase in MSE on the left and increase in node purity on the right, on the response of oak seedling density. Predictor variables are: mid_BA = total midstory basal area, SLOPE = slope class, mesic_BA = mesic species midstory basal area, ASPECT = aspect class, oak_BA = oak midstory basal area, O_BA = total overstory basal area, YRS = number of years since the last burn, BURN_NUM = total number of burns, TPA = overstory density class and SI = site index class.

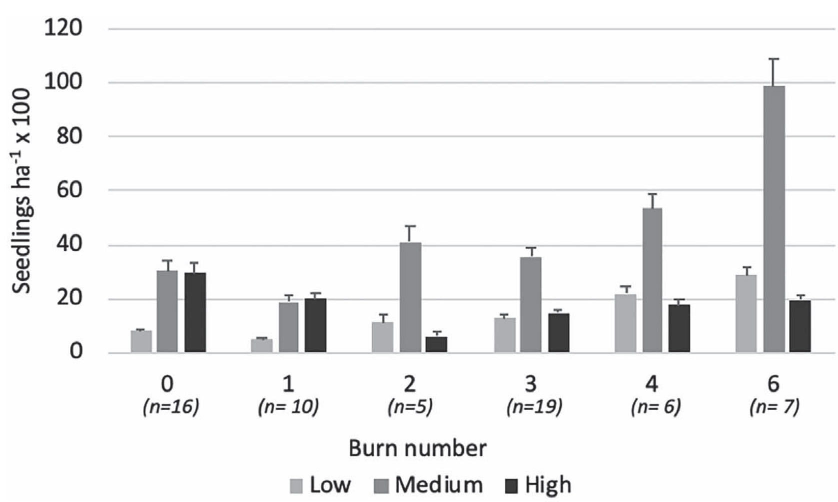

Figure 6 All oak species seedling density (seedlings ha^{-1} × 100) for low, medium and high percent slope categories displayed by the total number of burns. Stand sample sizes for each burn class are shown in italics below the *x*-axis, and error bars are displaying the standard error of the mean.

Longer time lags favour mesic species over oak

Composition within the regeneration layer shifted with the lag since last application of prescribed fire. This shift is quite relevant to oak management as many managers have great difficulty maintaining a reasonable burn schedule on many sites due to personnel, budgetary, weather and other influences outside of their control. The amount of time since the last burn significantly affected overall, oak and mesic species seedling densities in this retrospective study, but those responses differed significantly. Oak seedling densities were higher than those found on control plots only within the first 3 years post-fire, while mesic seedling densities were opposite those of oak (Figure 4) and were higher than control plots only in stands burned at least 4 years prior. Additionally, as the density of white oak became proportionally lower as the time between fires increased, mesic species density proportionally increased four- to sixfold (Table 3). This inverse relationship for both absolute and proportional densities between oak and mesic species becomes especially pronounced around 4 years post-fire.

The switch in dominance from oak to mesic regeneration is a common occurrence, but there is a lack of consensus as to when that switch happens. Stratton (2007) found that a 5 year return interval was too short for competitive oak regeneration to form before the next fire; but, in another study, oak seedling density did not increase in the first 2 years post-fire (Apsley and McCarthy, 2004). Although most seedling species suffer mortality after a burn and take more than 1 year to re-establish (Dolan and Parker, 2004), the spatial patchiness of many surface fires, as applied in oak-dominated stands, could allow many seedlings to escape top-killing as a direct effect of fire and, instead, have only injuries that lead to delayed mortality (Arthur *et al.,* 2015; Abella *et al.,* 2021). This lack of consensus highlights the importance of prescribed fire studies focusing not just on total burn numbers, but also the spacing between the burns or spacing between the last burn and time of sampling. Additionally, there is recent evidence that prescribed surface fire can enhance acorn survival and germination (Greenler *et al.,* 2020). This suggests that pairing fire with oak mast seeding events, which can often be difficult to predict (Sork, 1993; Sork and Bramble, 1993) especially across vast spatial scales (LaMontagne *et al.,* 2020), may best promote oak seedling regeneration and retention.

The random forest model results also suggested that the number of applications of prescribed fire (burn number) was quite influential and years since burn somewhat influential on oak seedling density. However, burn number and years since burn are confounded, which has been previously noted as an issue with study design in planned experiments (Arthur *et al.,* 2015) and in retrospective analyses (Mann *et al.,* 2020). Despite the confoundment, it is clear that managers need to consider both these elements of fire prescriptions in order to impact overall and oak seedling densities, as these burn variables may be as or more important than many topographic and structural variables. Prescribed fire in a mature stand in the Central Hardwood Region produces patchy and inconsistent results at best, as controlled burns rarely, if ever, cause significant overstory mortality. The heterogeneous impact of surface fire on regeneration (as reviewed in Brose *et al.,* 2005), coupled with the retrospective nature of this study, likely diminished the importance of both burn variables.

Topography and stand structure variables can override fire effects on regeneration

Although burn number was influential, several stand structure and topographic variables also affected oak seedling density. Overall, slope was one of two most influential predictors of oak reproduction density (Figure 5). Slope generally influences fire duration and intensity, which in turn influences species composition. As a surface fire progresses, it pre-heats material upslope leading to faster and potentially more intense combustion on steeper slopes. For example, the upslope side of mature trees are usually more damaged than the downslope side (Barnes and Van Lear, 1998), while trees on ridgetops often suffer the most damage because the fire has had time to gain intensity while moving upslope (Elliott *et al.,* 1999). The nature of fire may have caused low oak seedling densities on sites with high slopes (Figure 6), considering these steep areas would consistently receive intense burns that would topkill most stems and, through repeat applications of fire, lead to lower survival of any species.

Aspect, however, was not an important predictor variable. Although aspect should influence fire behaviour in a broad sense (Pyne *et al.,* 1996), the magnitude of its effect in these forests does not always impact mature trees (Stanis *et al.,* 2019). Additionally, seedlings require analyses at a finer spatial scale than mature overstory trees (Mason and Lashley, 2021), so microsite heterogeneity within each plot may have contributed to this lack of importance. Furthermore, the seedlings measured in this study were quite young and their presence on a mesic slope at this stage does not necessarily equate to long-term establishment, further diminishing the importance of aspect.

Midstory and overstory basal area variables (overstory BA, midstory BA, oak BA and mesic BA) were important and significant predictors of oak seedling density. The shade intolerance of oak and shade tolerance of maple (Burns and Honkala, 1990), is a contributing factor to reduction of oak dominance in many forests of the CHR (Nowacki and Abrams, 2008), so it is not surprising that mid- and overstory basal area partially controls oak seedling density. Furthermore, an increase in light, caused by gap-creation, in concert with prescribed fire usage has been shown to best benefit the oak reproduction layer (Izbicki *et al.,* 2020; however, see Kellner *et al.,* 2016). This effect of mid- and overstory BA on oak seedling regeneration has been established (Paquette *et al.,* 2006; Keyser and Loftis, 2015), so midstory thinning is often used to specifically promote oak establishment and growth (Lhotka and Loewenstein, 2009).

Future work

The continued lack of research centred on prescribed fire effects on non-timber attributes, as compared to effects of wildfire, will continue to hamper its use in eastern forests (Hiers *et al.,* 2020; Roces-Díaz *et al.,* 2021). Managers need guidance for assessment of the ecological tradeoffs for fire prescriptions built for oak regeneration goals with the potential detrimental impacts of that prescription on wildlife and other non-timber attributes. For example, in much of the Central Hardwood Region, the prescribed fire burn seasons are considerably shortened because of perceived, yet not fully proven, fire impacts on threatended and endangered bat communities (Boyles and Aubrey, 2006) and some herpofauna (Ford *et al.,* 2010; O'Donnell *et al.,* 2015). Fire impacts on forest floor communities, water provisioning and belowground soil processes in many forest types are also understudied (Roces-Díaz *et al.,* 2021). Additionally, Alexander *et al.* (2021) posit that our understanding of how fire effects vary with factors like climate change must improve in order to appropriately use prescribed burns for restoration goals in many forests. Future studies should focus on these thematic fields to further promote our understanding of how prescribed burning can be used to conserve ecologically important habitats such as the oak forests in the Central Hardwood region.

Conclusion

Years of research has prompted wider prescribed fire use to promote oak regeneration (Brose *et al.*, 2013; Brose *et al.*, 2014), yet consistent results continue to elude managers. This observation is particularly relevant to more mesic sites and forests of the Central Hardwood Region of the United States, as many of the published approaches were developed for more xeric sites typical in the Missouri Ozarks (Knapp *et al.*, 2015; Kinkead *et al.*, 2017) or mountainous regions of the Mid-Atlantic (Green *et al.*, 2010; Schwartz *et al.*, 2016). Despite this being a retrospective study and statistically unbalanced in design, we observed two major outcomes relative to oak management in the Central Hardwood Region. Firstly, prescribed fire may initially condition a site for oak regeneration, but only multiple burns (≥3 times) at high temporal frequency (≤4 years between burns) will lead to successful regeneration outcomes. Secondly, topography and, more importantly, overstory and midstory structure can override the direct effects of prescribed fire on regeneration. In this regard, a more efficient approach to develop oak regeneration may be to initially target the mesic midstory species with mechanical or chemical removal (Lhotka and Loewenstein, 2009; Motsinger *et al.*, 2010; Parrott *et al.*, 2012; Craig *et al.*, 2014) before prescribed fire is implemented on the site.

In conclusion, we would encourage managers and researchers aiming to improve prescribed fire science and knowledge to engage with minimum reporting standards to better catalogue fire behaviour and effects (Bonner *et al.*, 2021). Enhanced reporting of fire location and timing, local ecology, burn characteristics and post-fire assessment/monitoring should be incorporated into experimental and management burns alike.

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Supplementary data

Supplementary data are available at *Forestry* online.

Conflict of interest statement

None declared.

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Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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