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Escaping the fire trap: Does frequent, landscape-scale burning inhibit tree recruitment in a temperate broadleaf ecosystem?

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ABSTRACT

Frequent prescribed burning is commonly used to restore and maintain open forest ecosystems in temperate broadleaf regions of the eastern United States. Repeated surface fires reduce the abundance of small woody stems through top-kill or mortality, with implications for age structure and ecosystem development. In this study, we quantified tree recruitment patterns over two decades across two landscape-scale studies in Missouri: the Missouri Ozark Forest Ecosystem Project (a control, with no burning) and the Chilton Creek Management Area (burned on 2–3 year fire return interval). Through time, frequent burning reduced the rate of ingrowth (i.e., new trees entering the overstory size class, defined as ≥11.4 cm diameter at breast height (DBH)), and the effect of burning on the ingrowth rate was consistent across site types (summits, exposed backslopes, protected backslopes, or upland waterways). Two decades of frequent burning reduced the abundance of scarlet oak (*Quercus coccinea*) in the ingrowth population. In the unburned control, the proportional abundance of mesic species such as red maple (*Acer rubrum*) and blackgum (*Nyssa sylvatica*) increased during the study period; frequent fire controlled the population of red maple but resulted in a similar increase in blackgum abundance in the ingrowth population of the burned area. Our results indicate that frequent burning affects the tree recruitment process in multiple ways: 1) reducing the source population for recruitment by reducing midstory abundance; 2) increasing probability of mortality or top-kill during the recruitment period. Fire-free periods may be necessary to allow eventual replacement of canopy trees in temperate broadleaf open forest ecosystems.

1. Introduction

Fire is an important disturbance that shapes forest ecosystems globally, with characteristics of the local fire regime mediating ecosystem function and controlling forest composition and structure (Mayer and Khalyani, 2011; Staver et al., 2011). Many regions experience frequent, low-severity surface fires that maintain low tree densities and promote fire-adapted tree species (Murphy and Bowman, 2012; Archibald et al., 2013; Prichard et al., 2017). Patterns of anthropogenic influence often align closely with fire regimes, as has been documented within the central United States (i.e., Central Hardwood Region) over the past few centuries (Guyette et al., 2002; Stambaugh et al., 2018). In this region, frequent fire regimes historically supported open forest ecosystems, such as savannas and woodlands, with both broadleaf (e.g., *Quercus* spp.) and conifer (e.g., *Pinus* spp.) species present (Hanberry et al., 2020). The period of fire suppression and exclusion initiated in the early 1900s resulted in increased tree densities and compositional shifts towards more fire-sensitive species (Nowacki and Abrams, 2008; Hanberry et al., 2014). During the past few decades, restoring open forest ecosystems through the use of frequent prescribed burning has become an important objective of many land managers (Guldin, 2019; Bragg et al., 2020).

Frequent fire affects a variety of ecosystem processes (Sturtevant and Hanberry, 2021), with its effects on tree mortality and regeneration important for maintaining the structure and composition of open forest ecosystems. Low-intensity surface fires act most strongly on small-diameter stems, reducing abundance of trees in the midstory layer through top-kill or mortality (Dey and Hartman, 2005; Keyser et al., 2018). Repeated fires can result in a 'fire trap', in which woody stems are maintained as sprouts but unable to recruit into larger size classes due to

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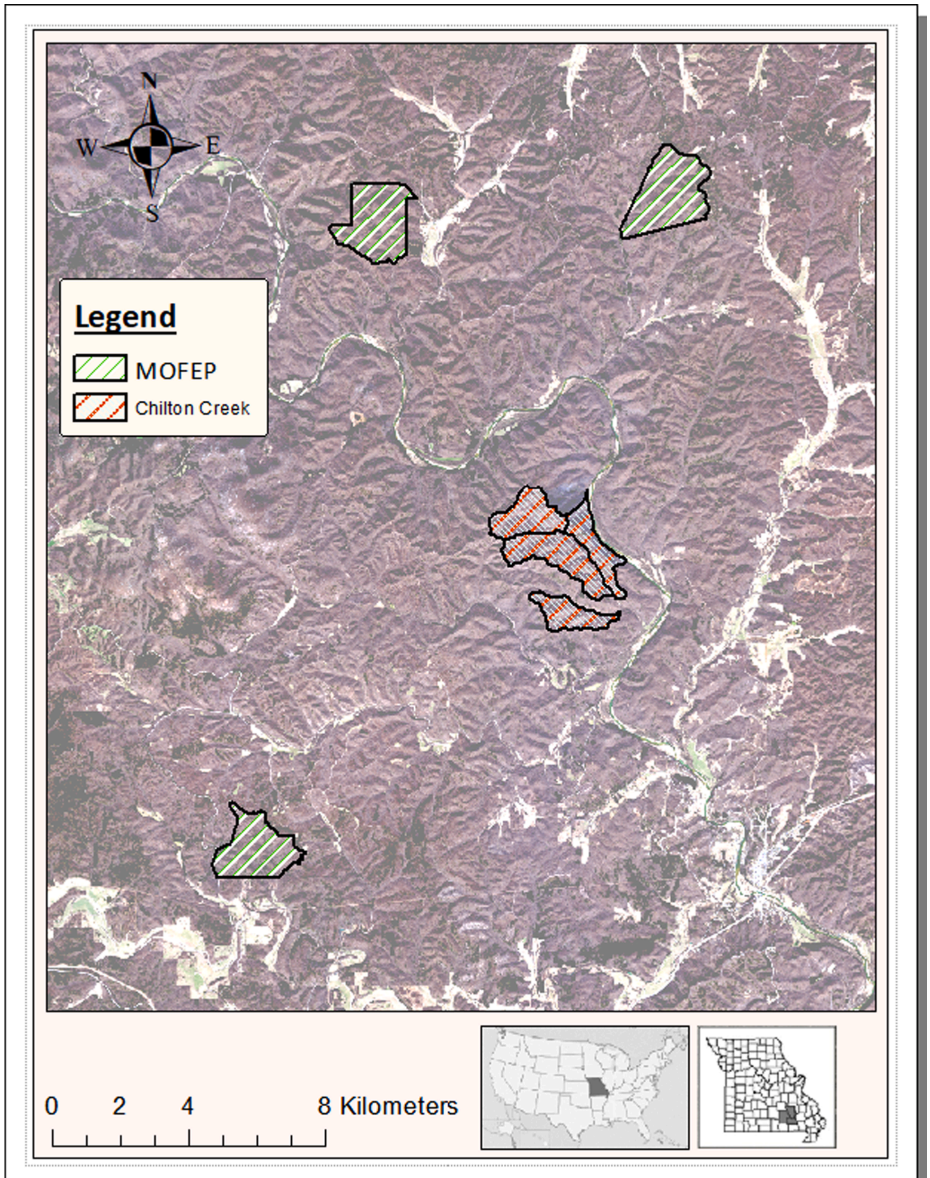

Fig. 1. Location of three experimental units at the unburned MOFEP site and four experimental units burned frequently at the CCMA site.

top-kill (Bond and Midgley, 2001; Grady and Hoffmann, 2012). Through time, repeated fires of this type can also cause mortality of overstory trees, although species vary in fire tolerance (Huddle and Pallardy, 1996). Consequently, structure typically becomes more open through time as repeated fire and other disturbances such as wind, drought, ice, insects, and disease reduce canopy density. Unlike disturbances that primarily impact overstory trees and therefore release understory vegetation and tree reproduction, frequent fire can prevent the recruitment of abundant stems into the midstory and overstory (Knapp et al., 2017).

The effects of fire on stand dynamics have important implications for age structure of open forest ecosystems. Concepts of uneven-aged, fire-maintained open forest ecosystems often guide restoration efforts (Mitchell et al., 2006; Hanberry et al., 2018) but are contingent on the recruitment of new trees that survive frequent fires to introduce younger age classes to the overstory. While this has been well-documented in frequent-fire conifer ecosystems dominated by longleaf pine (*Pinus palustris*) (e.g., Platt et al., 1988), recruitment of broadleaf species like oaks common to the Central Hardwood Region is reported to require fire-free periods that exceed a decade (Arthur et al., 2012). Consequently, this raises questions as to whether frequent prescribed burning used for managing open forest structure also allows opportunities for tree recruitment and the development of uneven-aged open woodlands in upland oak ecosystems.

Tree recruitment (i.e., the ascension of saplings into the overstory (Dey, 2014)) in ecosystems with frequent surface fire is largely controlled by fire's effects on small-diameter trees. Energy transfer through convection can damage buds and branches, and the location of these tissues on small trees may easily result in damage from surface fires. Surface fires can also cause damage to the cambium and conductive tissues of tree stems, resulting in mortality or top-kill followed by resprouting (Hood et al., 2018). Small-diameter trees are particularly vulnerable to this damage, because their bark is relatively thin; as tree diameter increases, bark thickness also increases and provides greater protection from fire (Pausas, 2015; Schafer et al., 2015). Tree species vary in the rate of bark development relative to stem size, resulting in a potential disturbance-based filter of species composition (Lawes et al., 2011; Schafer et al., 2015).

The likelihood of tree recruitment occurring with frequent surface fire is therefore related to the growth rate of individual trees (to reach a

Table 1
Schedule of prescribed fires applied by unit at CCMA. The mean fire interval represents average number of years between fires for each unit.

Year	Chilton East	Chilton North	Chilton South	Kelly South
1998	2-Apr	13-Mar	26-Mar, 23-Nov	6-Apr
1999				
2000			7-Mar	6-Mar
2001				10-Mar
2002	30-Mar	6-Mar		
2003	11-Mar		15-Mar	
2004		27-Feb		28-Feb
2005	30-Nov			
2006				
2007		6-Mar	6-Mar	
2008				7-Apr
2009	18-Mar		18-Mar	
2010				
2011		13-Mar	12-Mar	1-Mar
2012				
2013	28-Mar	1-Apr	3-Apr	3-Apr
2014	10-Mar		6-Feb	
2015		16-Mar		30-Mar
2016	5-Mar		5-Mar	
2017		9-Mar		16-Mar
Total fires (20 years)	8	8	10	9
Mean Fire Interval	2.6	2.6	2.1	2.3

size resistant to top-kill or mortality) and the local conditions of the fire (e.g., fire intensity around the individual tree) (Wakeling et al., 2011; Hoffmann et al., 2020). Competition from overstory trees reduces the growth rate of individuals in the understory (Vickers et al., 2014), such that growth to a fire-resistant size would be expected to occur sooner with more open structure. Across the landscape, variation in site productivity can further affect growth rates, with expectations that sites of greater productivity will reach sizes resistant to top-kill or mortality faster than lower productivity sites. Therefore, patterns in tree recruitment in relation to fire regime may vary across productivity gradients. Physical conditions and stand characteristics associated with site productivity can also affect variation in fire behavior at the landscape-scale (Iverson et al., 2004; Stambaugh and Guyette, 2008). Variation in the fire behavior experienced by individual trees, including local occurrence of low-intensity fire behavior due to discontinuous fuels or local changes in fuel moisture, can provide opportunity for tree recruitment despite general patterns of top-kill or mortality (Hoffmann et al., 2020).

Despite its importance to long-term stand dynamics and age structure, effects of frequent fire on tree recruitment are not well-described in open forest ecosystems of temperate broadleaf regions. In this study, we utilize two long-term, landscape-scale field experiments to contrast tree recruitment patterns with and without frequent prescribed burning. For our first two study objectives, we describe the patterns of ingrowth (defined as tree recruitment into the overstory size class (trees ≥ 11.4 cm diameter at breast height; DBH)) through time in relation to prescribed burning and site type:

Objective 1) Determine the effect of frequent prescribed burning on the amount and composition of ingrowth over approximately two decades.

Objective 2) Evaluate site effects on patterns of ingrowth through time.

We hypothesize that frequent burning will result in a reduction in ingrowth through time but will favor fire-tolerant species (H1). We hypothesize that this pattern will vary across site types when landscape-scale burning is applied (H2). Given that tree recruitment rates are expected to vary with stand structure, we examine how prescribed burning affects relationships between stand structure and ingrowth abundance and survival:

Objective 3) Quantify relationships between the rate of ingrowth and independent variables of: a) overstory basal area and b) midstory ($3.8 \leq$ DBH < 11.4 cm) stem abundance with and without frequent prescribed fire.

Objective 4) Determine effects of overstory basal area on survival probability of new ingrowth throughout the duration of the study period with and without frequent prescribed fire.

We hypothesize that overstory basal area will be negatively related to the rate of ingrowth and to the survival of ingrowth, but frequent

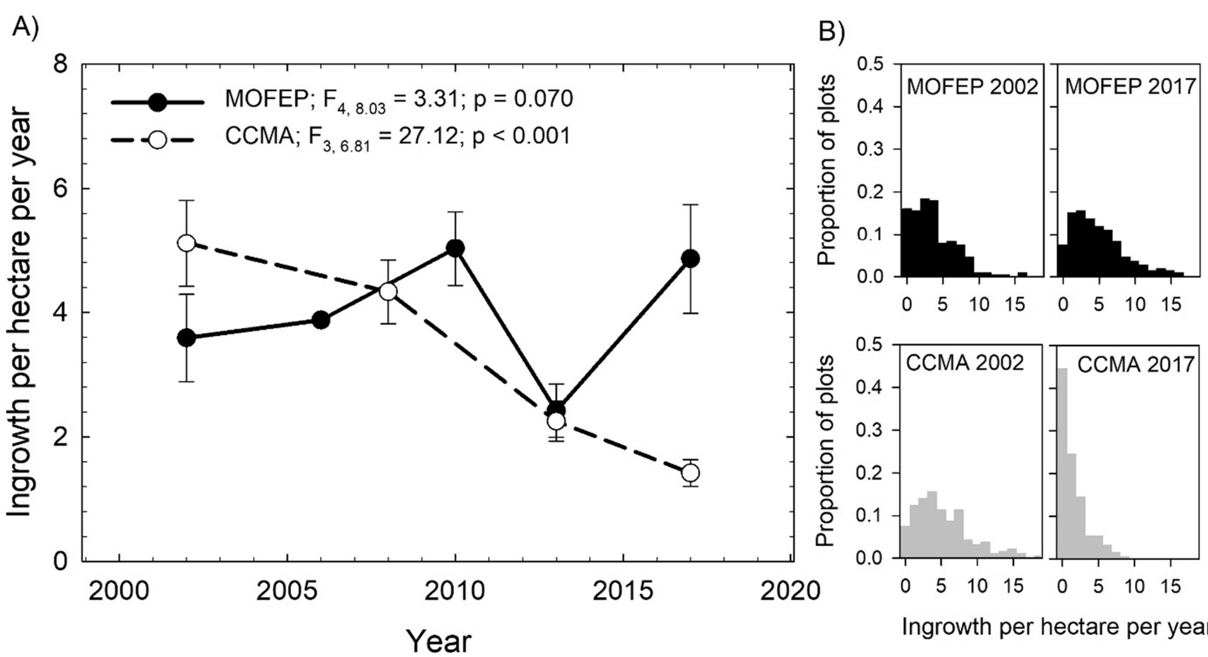

Fig. 2. A) Number of trees per hectare (mean ± one standard error) entering the overstory size class ($\geq$11.4 cm diameter at breast height (DBH)) per year at the MOFEP study sites (unburned control) and at the CCMA study sites (frequent burning), calculated for each sampling interval. B) Frequency distribution of ingrowth per hectare per year across all plots for the first sampling interval and the last sampling interval at each study site. Prescribed burning started at CCMA in 1998, with the initial sampling year being 1998 at both studies.

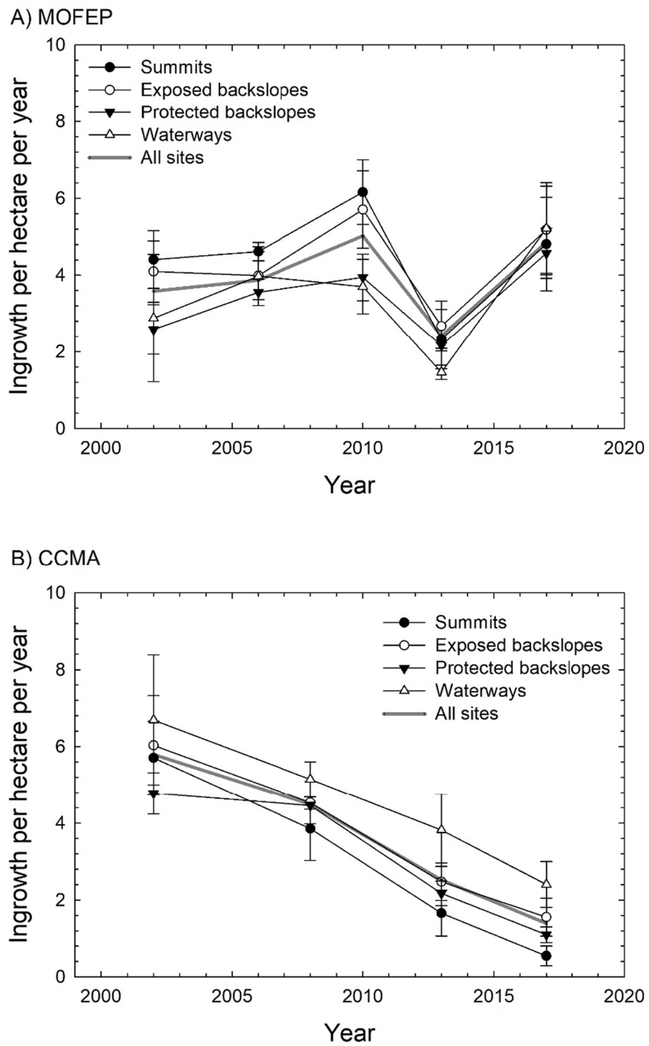

Fig. 3. Number of trees per hectare (mean ± one standard error) entering the overstory size class (≥11.4 cm diameter at breast height (DBH)) per year for common site types at A) the MOFEP study sites (unburned control) and B) the CCMA study sites (frequent burning), calculated for each sampling interval. Prescribed burning started at CCMA in 1998, with the initial sampling year being 1998 at both studies.

prescribed fire will reduce the abundance and survival of ingrowth consistently across basal area levels (H3). In addition, we hypothesize a positive relationship between the abundance of midstory stems and the abundance of ingrowth, with a stronger relationship with frequent prescribed burning than in unburned areas (H4). Reductions in the abundance of the midstory population would remove the 'source population', or the population of trees available to grow into the overstory size class during the recruitment process. Because we expect prescribed burning to act strongly on small-diameter woody stems (i.e., the midstory population), we will:

Objective 5) Determine effects of frequent prescribed burning on the abundance and composition of midstory saplings.

We hypothesize that frequent burning acts to eliminate the source population for tree recruitment through time (H5).

2. Methods

2.1. Study site

We analyzed data from two landscape-scale studies located in the Current River Hills ecological subsection of southeastern Missouri, USA (Fig. 1). The Missouri Ozark Forest Ecosystem Project (MOFEP) and the Chilton Creek Management Area (CCMA) are located within the same landscape, with study areas within 15 km of each other. The area features moderately rolling to deeply dissected terrain with local relief ranging from 50 to 150 m and elevations of 150–300 m above sea level (Kabrick et al., 2000). Bedrock formations include the Roubidoux formation, which includes interbedded sandstone, sandy dolostone, quartzose, and chert; the Gasconade formation, in which the upper half of the formation includes thick beds of coarsely crystalline dolostones interbedded with chert and the lower half of the formation includes finely crystalline dolostone with few chert nodules and a bed of sandstone and quartzose from 1 to 3 m thick at its base; and the Eminence-Potosi formation with thick beds of coarsely crystalline dolostone (Meinert et al., 1997). During the study period (1 January 1997 through 31 December 2017), mean annual precipitation was 1098 mm. Mean monthly maximum temperature was 32.2 °C in July, and mean monthly minimum temperature was −6.0 °C in January (National Climate Data Center, station USC00231674, Clearwater Dam, MO).

The upland forests of the study region are dominated by oak species, and the structure and composition of MOFEP and CCMA were similar at the start of the study. In 1997, mean overstory (trees ≥ 11.4 cm DBH, measured at 1.37 m height) basal area was 20.6 m^2/ha at MOFEP and 15.2 m^2/ha at CCMA, and the mean number of overstory trees per hectare was 387.1 at MOFEP and 376.4 at CCMA. Overstory composition was dominated by a few common species, with eight species making up ≥ 90% of the overstory basal area. Black oak (*Quercus velutina*) was the most abundant species, with 28.0% of the basal area at MOFEP and 26.9% of the basal area at CCMA, followed by scarlet oak (*Q. coccinea*; 24.2% at MOFEP; 17.2% at CCMA) and white oak (*Q. alba*; 18.6% at MOFEP; 21.0% at CCMA). The remaining most abundant species, each with < 10% of the basal area, included shortleaf pine (*Pinus echinata*), post oak (*Q. stellata*), pignut hickory (*Carya glabra*), and mockernut hickory (*Carya tomentosa*) at both sites, as well as black hickory (*Carya texana*) at MOFEP and northern red oak (*Quercus rubra*) at CCMA.

2.2. Experimental design

The MOFEP is a long-term, landscape-scale field experiment that is maintained by the Missouri Department of Conservation (MDC) (Shifley and Brookshire, 2000; Knapp et al., 2014). It was designed to evaluate forest management effects on a variety of ecosystem responses using a robust experimental design and treatments representative of MDC forestry operations (Sheriff and He, 1997). The MOFEP study uses a randomized complete block design, with three replicate blocks. Each block includes three treatments: even-aged management, uneven-aged management, and no harvest management, each of which is applied to management compartments (the experimental unit), that range from 300 to 500 ha. Within the even-aged management and uneven-aged management treatments, forest management is applied to stands within compartments following MDC practice (Knapp et al., 2014). Fire is not used in the MOFEP study; consequently, the no harvest management treatment at MOFEP represents a control treatment with no prescribed burning and no other management activities. There are three replicate compartments of the no harvest (i.e., unburned control) treatment at MOFEP.

The CCMA is owned by The Nature Conservancy and managed in collaboration with MDC as a long-term, landscape-scale prescribed fire study. The CCMA includes four compartments to which prescribed burns are applied separately at random periodic intervals that range from 1 to 4 years. This burn frequency is commonly used in restoring and maintaining open structure and enhancing ground flora diversity in woodlands of the region (Bragg et al., 2020). To determine the burn schedule for each compartment, a burn interval from 1 to 4 years is randomly determined at the time that a compartment gets burned; therefore, the burn schedule for each compartment is independent of the other compartments, and each specific burn interval is randomly determined. The

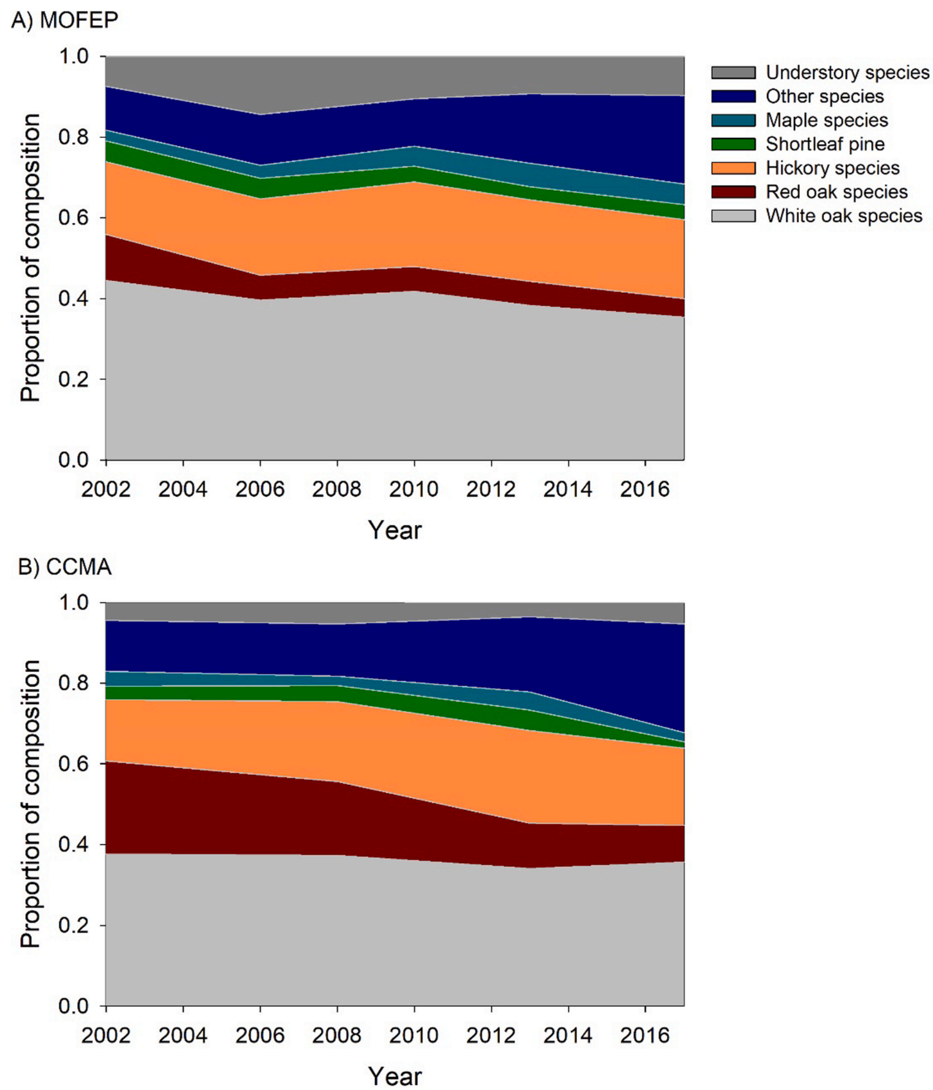

Fig. 4. Proportional abundance of ingrowth population by species groups during each sampling interval at A) MOFEP and B) CCMA.

overall mean fire return interval across the four compartments was 2.4 years, with variation in burn years among all compartments (Table 1). Most prescribed burns occurred from February – April, although fall burning was occasionally used. Generally, ignition was done along compartment boundaries, with interior ignition along strategic topographic features (typically ridges), allowing the fire to burn through the compartments but with no efforts to ensure complete burning everywhere. Burn plans allowed day-of-burn weather conditions to range from −1 to 27 °C air temperature, 25 to 70% relative humidity, and 8 to 32 km/hr midflame windspeeds (Maginel et al., 2019).

The CCMA was designed as a parallel study to MOFEP, using the MOFEP no harvest treatments as unburned controls. At each study, the compartment is the experimental unit, with three replicates of the unburned control treatment at MOFEP and four replicates of the periodic prescribed burning treatment at CCMA. Compartments were delineated into Ecological Land Types (ELTs) based on Ecological Classification System (ECS) used by MDC (Nigh et al., 2000). In this system, ELTs are characterized based on landform position, aspect, and soils (Supplemental Table S1). Plots for sampling vegetation were stratified to represent the proportional abundance of ELTs within each compartment, with plot locations randomly assigned within each ELT (Brookshire and Dey, 2000). At MOFEP, there were 70, 71, and 76 sample plots within each of the three respective experimental units, and at CCMA there were 22, 44, 78, and 43 sample plots within the four experimental units (Supplemental Table S1).

2.3. *Data collection*

Each sample plot was a fixed-area, circular 0.2 ha plot, with smaller fixed-area plots nested for sampling different size classes of vegetation. All overstory trees were surveyed, with each tree numbered with a unique aluminum tag and species and DBH recorded. Trees were marked as ingrowth when first encountered within the overstory size class (≥11.4 cm DBH). Vegetation within the midstory size class (3.8 ≤ DBH < 11.4 cm) was surveyed within four 0.02 ha, circular sub-plots in each overstory plot. Midstory plots were located 17 m from plot center in each cardinal direction. Within each sub-plot, the DBH and species of each midstory tree was recorded, but trees were not tagged for individual repeated measurements. Sampling occurred in the dormant season (typically October through March). There were six sampling periods at MOFEP (with the sampling ending in 1998, 2002, 2006, 2010, 2013, and 2017) and five sampling periods (with the sampling ending in 1998, 2002, 2008, 2013, and 2017) at CCMA.

2.4. *Data analysis*

For all analyses, ingrowth was defined as the number of new trees per hectare entering the overstory size class during a defined period of time,

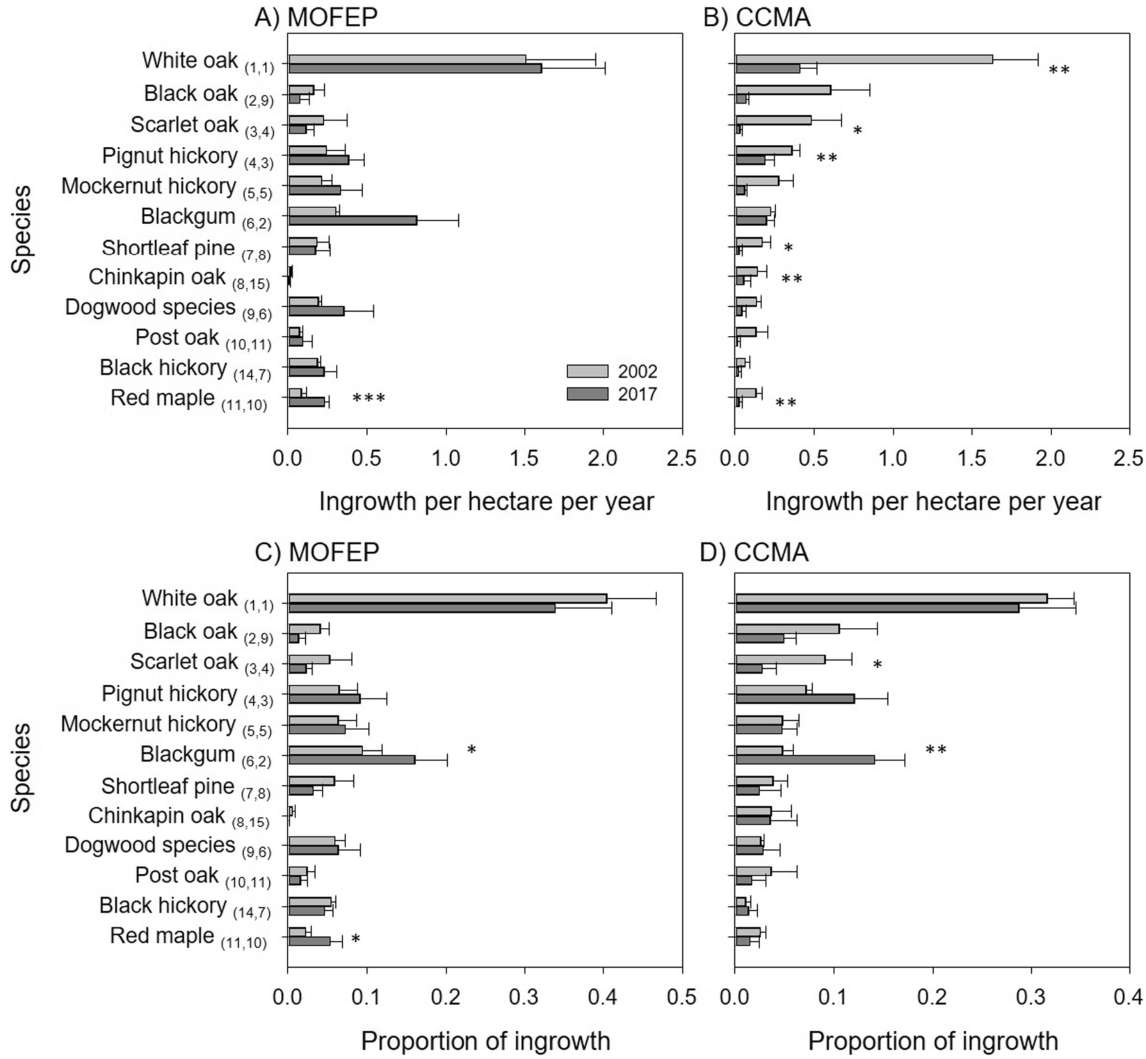

Fig. 5. Ingrowth per hectare per year (panels A and B) for the top ten most common species in the first and last sampling interval at MOFEP and CCMA. Ranks based on species abundance in the first sampling interval are provided in parentheses, with the first value being the abundance ranking at CCMA and the second value being the abundance ranking at MOFEP. The proportion of the ingrowth population contributed by each species during each sampling interval is provided in panels C and D, with asterisks indicating statistical significance of the matched-pairs t-tests for each species within each panel. *$p < 0.1$; **$p < 0.05$; ***$p < 0.01$. Species names are white oak (*Quercus alba*), black oak (*Q. velutina*), scarlet oak (*Q. coccinea*), pignut hickory (*Carya glabra*), mockernut hickory (*C. tomentosa*), blackgum (*Nyssa sylvatica*), shortleaf pine (*Pinus echinata*), chinkapin oak (*Q. muehlenbergii*), dogwood species (*Cornus* spp.), post oak (*Q. stellata*), black hickory (*C. texana*), and red maple (*Acer rubrum*).

usually reported per year. We focus on this tree size because it was the smallest size at which individual trees were tracked and because previous studies have shown frequent prescribed burning to completely eliminate trees of this size from hardwood ecosystems after several decades of burning (Knapp et al. 2015; Knapp et al. 2017). To address Objective 1, we used generalized linear mixed models to quantify changes in ingrowth through time by calculating ingrowth at each sampling period. Because the sampling dates differed between the unburned study (MOFEP) and the burned study (CCMA), we modeled the effect of year on ingrowth separately for each study. We used generalized linear mixed models with a normal distribution, with year as a fixed effect in a repeated measures design using a compound symmetry covariance structure. Random effects in the model included plots (the sub-sample within each study design), the compartments (the experimental unit of each study), and the plots nested within compartments.

For Objective 2, we classified plots into common groups within the ecological site classification, primarily based on slope position and aspect. The ecological land types were grouped into four site types: summit, exposed backslopes, protected backslopes, and waterways (Supplemental Table S1). Due to low sample sizes across the two studies, we excluded plots that were in sinkholes, benches, and footslopes. The dataset for Objective 2 included 195 plots from MOFEP and 159 plots from CCMA. Similar to Objective 1, we used generalized linear mixed models with a normal distribution to test for fixed effects of site type, year, and interactions between site type and year. Random effects in the model included plots, the compartments, plots nested within site types, and site types nested within compartments.

Change in species composition through time was analyzed using paired t-tests for the ten most common species in the ingrowth population from each study during the first sampling interval. For each of these species, we tested if the difference between the abundance in the first sampling interval and the abundance in the last sampling interval was significantly different from zero. Analyses were conducted for the number of ingrowth per hectare per year and for the proportional abundance of ingrowth as dependent variables for each species. In addition, we described proportional abundance of common species groups through time for the ingrowth population and the midstory population. Species groups include: white oak group (e.g., *Quercus alba,*

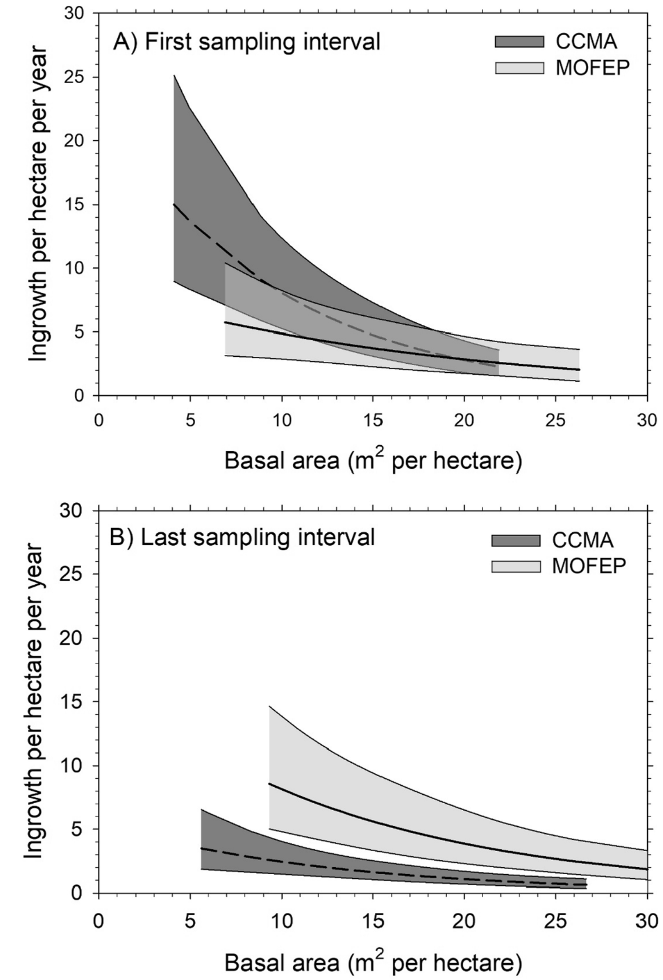

Fig. 6. Predicted mean with confidence intervals (shaded) of relationship between basal area (m^2 per hectare) and the number of ingrowth stems per hectare per year for A) the first sampling interval and B) the last sampling interval at each study site.

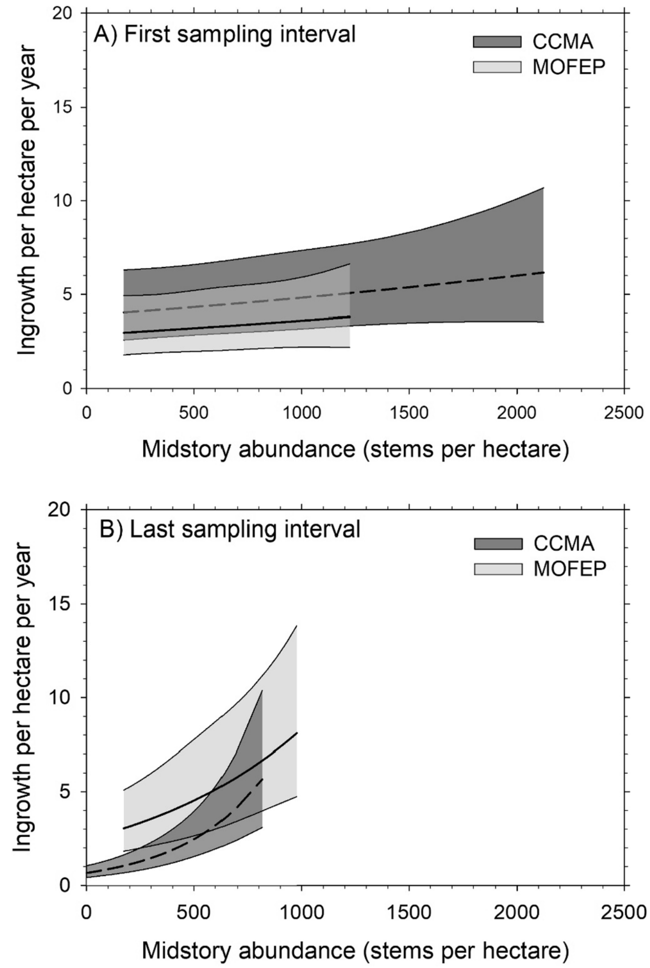

Fig. 7. Predicted mean with confidence intervals (shaded) of relationship between the abundance of midstory stems (3.8 ≤ DBH < 11.4 cm) and the number of ingrowth stems per hectare per year for A) the first sampling interval and B) the last sampling interval at each study site. The scaling of the x-axes was kept constant for the two panels for visual contrast.

Q. stellata, Q. muehlenbergii), red oak group (e.g., *Quercus coccinea*, *Q. marilandica*, *Q. rubra*, *Q. velutina*), hickory species (e.g., *Carya cordiformis*, *C. glabra*, *C. ovata*, *C. texana*, *C. tomentosa*), shortleaf pine (*Pinus echinata*), maple species (e.g., *Acer negundo*, *A. rubrum*, *A. saccharum*), other overstory species (e.g., *Celtis occidentalis*, *Diospyrus virginiana*, *Fraxinus* spp., *Juglans nigra*, *Nyssa sylvatica*, *Platanus occidentalis*, *Prunus* spp., *Ulmus* spp.), and understory species (e.g., *Amelanchier arborea*, *Cercis canadensis*, *Cornus* spp., *Juniperus virginiana*, *Ostrya virginiana*, *Rhus* spp.).

To address Objective 3, we modeled the relationships between ingrowth and the independent variables of a) stand basal area and b) midstory stem abundance. With interest in the effects of frequent prescribed burning on these relationships, we modeled these relationships separately for the earliest sampling interval (no accumulated effects of frequent prescribed burning) and for the last sampling interval (including accumulated effects of frequent prescribed burning). Because the two studies had the same sampling years for the earliest and latest interval and had the same total study durations (19 years), the datasets from each study were combined for analyses. We used generalized linear mixed models with ingrowth as the dependent variable and fixed effects including stand basal area or midstory abundance, the study (MOFEP or CCMA), and the interaction of stand basal area or midstory abundance with the study. The models were fit using a negative binomial distribution with a log link function. Random effects in the model included the compartment, plots nested within compartment, and compartments nested within study. Model predictions with 95% confidence intervals of the means were generated for the fixed effects to display relationships.

For individual trees of the ingrowth population during the first sampling interval, we modeled the probability of survival through the duration of the study (15 years through the last sampling period; Objective 4). Survival was defined as persistence without top-kill (i.e., stems remaining in the overstory size class). We used generalized linear mixed models, with a binomial distribution and a logit link function, with fixed effects of basal area during the final sampling period, the study (MOFEP or CCMA), and the interaction of basal area and the study. We specified random intercept terms for individual trees nested within plots, compartments, plots nested within compartments, and compartments nested within study. Models were run for all species grouped together, and separate models were run for each species group.

The analysis for Objective 5 was similar to that for Objective 1. To quantify changes in the abundance of midstory stems through time, we used generalized linear mixed models with a normal distribution, with year as a fixed effect in a repeated measures design using a compound symmetry covariance structure. Random effects in the model included plots, the compartments, and the plots nested within compartments. Because fire is likely to differentially affect trees across the range of tree sizes within the midstory population (3.8–11.4 cm DBH), we generated frequency distributions of midstory abundance by 1-cm diameter classes for each sampling year at the two study sites.

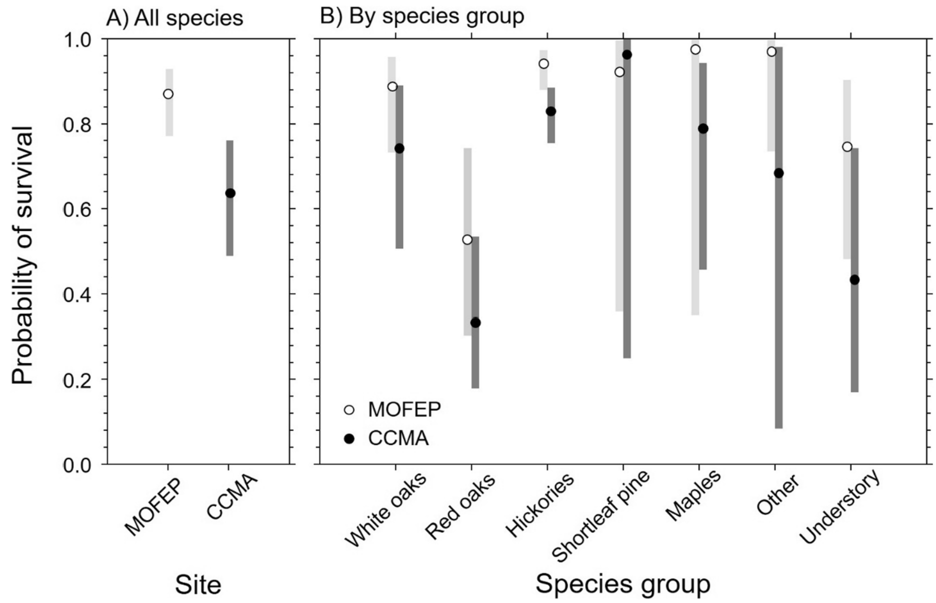

Fig. 8. Probability of survival (predicted mean and 95% confidence interval) at the last sampling for an ingrowth tree encountered during the first sampling, representing a 15-year period for both the unburned (MOFEP) and burned (CCMA) landscapes, showing A) all species and B) separation by species groups.

3. Results

3.1. Patterns in tree recruitment through time

During the 19-year study period, the total number of trees that recruited into the overstory did not differ between the unburned MOFEP study and the frequently burned CCMA ($F_{1,\ 4.19} = 2.51$; p = 0.185), averaging 76.6 trees per hectare (4.0 trees per hectare per year) at MOFEP and 63.8 trees per hectare (3.4 trees per hectare per year) at CCMA. The number of ingrowth trees per hectare per year was consistent through time at MOFEP ($F_{4,\ 8.03} = 3.31$; p = 0.070) but decreased through time at CCMA ($F_{3,\ 6.81} = 27.12$; p < 0.001; Fig. 2A). During the first measurement interval at CCMA, there were 5.1 ingrowth trees per hectare per year, and during the last measurement interval there were 1.4 ingrowth trees per hectare per year (Fig. 2A). During the last sampling interval at CCMA, 45% of the plots had no ingrowth, with 84% of the plots having<3 ingrowth trees per hectare per year. In contrast, only 7% of plots had no ingrowth during the last interval at MOFEP, with 62% of plots having 3 or more ingrowth trees per hectare per year (Fig. 2B). We found no significant interaction effects on ingrowth between the common site types (summits, exposed backslopes, protected backslopes, and waterways) and year for either MOFEP ($F_{12,\ 38.92} = 0.48$; p = 0.915) or CCMA ($F_{9,\ 27.50} = 0.64$; p = 0.756), and the temporal patterns in the abundance of ingrowth through time were similar for each of the site types (Fig. 3).

The species composition of the ingrowth population was generally stable through time and similar between the two studies (Fig. 4), with approximately 40% of all ingrowth stems being species in the white oak group. At CCMA, the species in the red oak group decreased from 23.1% to 9.1% of the ingrowth population, and the “other” species group increased from 12.6% to 26.9% of the ingrowth population during the study period. The same general trend occurred at MOFEP, with species in the red oak group decreasing from 11.4% to 4.6% of the ingrowth population and the “other” species group increasing from 10.8% to 21.9% of the ingrowth population during the study period. At CCMA, there were significant decreases in the abundance of ingrowth of red maple, pignut hickory, shortleaf pine, white oak, scarlet oak, and chinkapin oak between the first and last measurement periods; at MOFEP, there was a significant increase in the ingrowth of red maple during the same period (Fig. 5). The decreases at CCMA generally reflect the overall reduction in the abundance of ingrowth, however, as the proportional contribution to the ingrowth population remained unchanged for most species. At both sites, the proportion of blackgum increased, and at CCMA the proportion of scarlet oak decreased in the ingrowth population (Fig. 5).

3.2. Drivers of recruitment: ingrowth and mortality

Stand basal area had a significant, negative relationship with the number of ingrowth trees for both studies during the first sampling interval ($F_{1,\ 359.6} = 32.07$; p < 0.001), with no significant interaction between study and basal area ($F_{1,\ 359.6} = 3.25$; p = 0.072; Fig. 6A). Although basal area ranged higher at MOFEP than at CCMA, the confidence intervals for the means overlapped throughout the common range, indicating no differences in the relationship between basal area and ingrowth between the two studies at that time. The ranges in basal area increased by the last sampling interval for both studies (Fig. 6B). Stand basal area still had a significant, negative relationship with the number of ingrowth trees ($F_{1,\ 386.8} = 32.05$; p < 0.001), and there was a significant difference in the ingrowth between studies ($F_{1,\ 63.7} = 4.20$; p = 0.045). Ingrowth at CCMA was lower than that at MOFEP, with no overlap in the confidence intervals for the means across the full range of basal area values (Fig. 6B).

During the first sampling period, there was no relationship between the abundance of midstory stems and the number of ingrowth trees ($F_{1,\ 399} = 1.51$; p = 0.220; Fig. 7A). The range of midstory abundance values at CCMA exceeded that at MOFEP, but patterns between the two sites were similar. By the last sampling interval, the range of values for abundance of midstory stems was reduced at CCMA but remained similar to the first sampling period at MOFEP (Fig. 7B). There was a significant interaction between the abundance of midstory stems and the study ($F_{1,\ 350.4} = 6.05$; p = 0.014), with the slope parameter at CCMA (coefficient estimate = 0.0026) twice as large as that at MOFEP (coefficient estimate = 0.0013).

For trees that occurred as ingrowth during the first sampling period, mean survival through the end of the study (the subsequent 15 years) was greater at MOFEP (87% probability of survival) than at CCMA (64% probability of survival) ($F_{1,133.1} = 3.97$, p = 0.048; Fig. 8A). There was no effect of stand basal area on the probability of survival ($F_{1,346.7} = 0.10$; p = 0.758) and no significant interaction between stand basal area

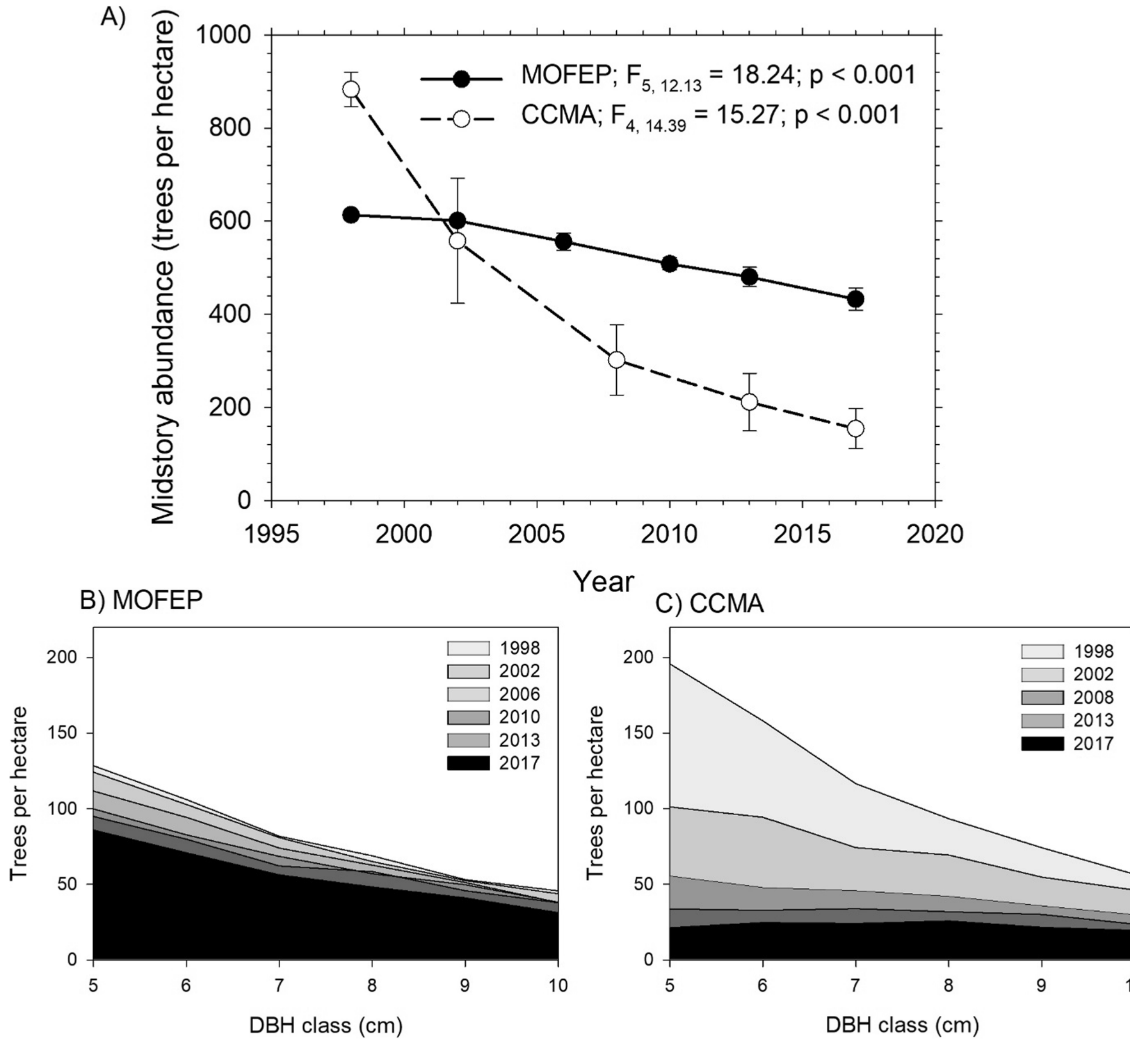

Fig. 9. A) Number of trees per hectare (mean ± one standard error) in the midstory (3.8 ≤ DBH < 11.4 cm) per year at the MOFEP study sites (unburned control) and at the CCMA study sites (frequent burning), calculated for each sampling interval. Frequency distributions by size class shown for each sample year for B) MOFEP and C) CCMA. Prescribed burning started at CCMA in 1998, with the initial sampling year being 1998 at both studies.

and the study ($F_{1,346.7} = 0.41$, p = 0.520). We also analyzed survival probability for each species group, finding no effects of stand basal area on survival probability for any species (p ≥ 0.401), no significant interaction between stand basal area and the study for any species (p ≥ 0.166), and no differences between the studies for any species (p ≥ 0.064). Species showed a range of survival probabilities, however, with the mean survival probability for shortleaf pine > 90% for both studies and mean survival probability for species in the red oak group < 55% for both studies (Fig. 8B). Low sample sizes for some species groups (e.g., shortleaf pine) resulted in poor confidence for model estimates.

After accounting for mortality, the total number of ingrowth per hectare that remained alive at the end of the study period was greater at MOFEP (70.7 trees (3.7 ingrowth trees per hectare per year)) than at CCMA (46.5 trees (2.4 ingrowth trees per hectare per year)) ($F_{1,\ 4.91} = 9.06$; p = 0.031).

3.3. Effects of frequent prescribed fire on sapling population

The abundance of midstory trees decreased through time at both MOFEP and CCMA (Fig. 9A). During the first sampling period, there were nearly 900 midstory trees per hectare at CCMA and just over 600 midstory trees per hectare at MOFEP. The decrease was gradual through time at MOFEP, with a significant difference from the abundance of midstory trees in 1998 first occurring in 2010 (p = 0.002). In contrast, the abundance of midstory stems decreased sharply through time following the initiation of frequent prescribed burning at CCMA, with significant reductions from 1998 to 2002 (p = 0.004) and from 2002 to 2006 (p = 0.013). Within the midstory population, small diameter trees were more abundant than large diameter trees at both MOFEP and CCMA during the first measurement period (Fig. 9). The decrease through time for the midstory population at MOFEP was proportional across the midstory size classes (1-cm dbh classes, from 5 to 10 cm dbh), ranging from 67 to 77% of the 1998 abundance present in 2017. At CCMA, the proportion of the 1998 midstory abundance present in 2017 increased with tree size, with 10.8%, 15.6%, 20.7%, 27.6%, 29.0%, and 34.4% of the 1998 abundance present in 2017 for the 5, 6, 7, 8, 9, and 10-cm dbh classes, respectively (Fig. 9B and C). Within the midstory population, the understory tree species group dominated the small diameter classes, with increasing abundance of white oak and hickory species in the larger diameter classes (Fig. 10). Frequent prescribed burning at CCMA resulted in reductions in the relative abundance of the red oak species group by the last sampling period, with the relative abundance of scarlet oak reduced from 4.3% to 0.7% and that of black oak reduced from 4.6% to 0.9% of the midstory population at CCMA from 1998 to 2017.

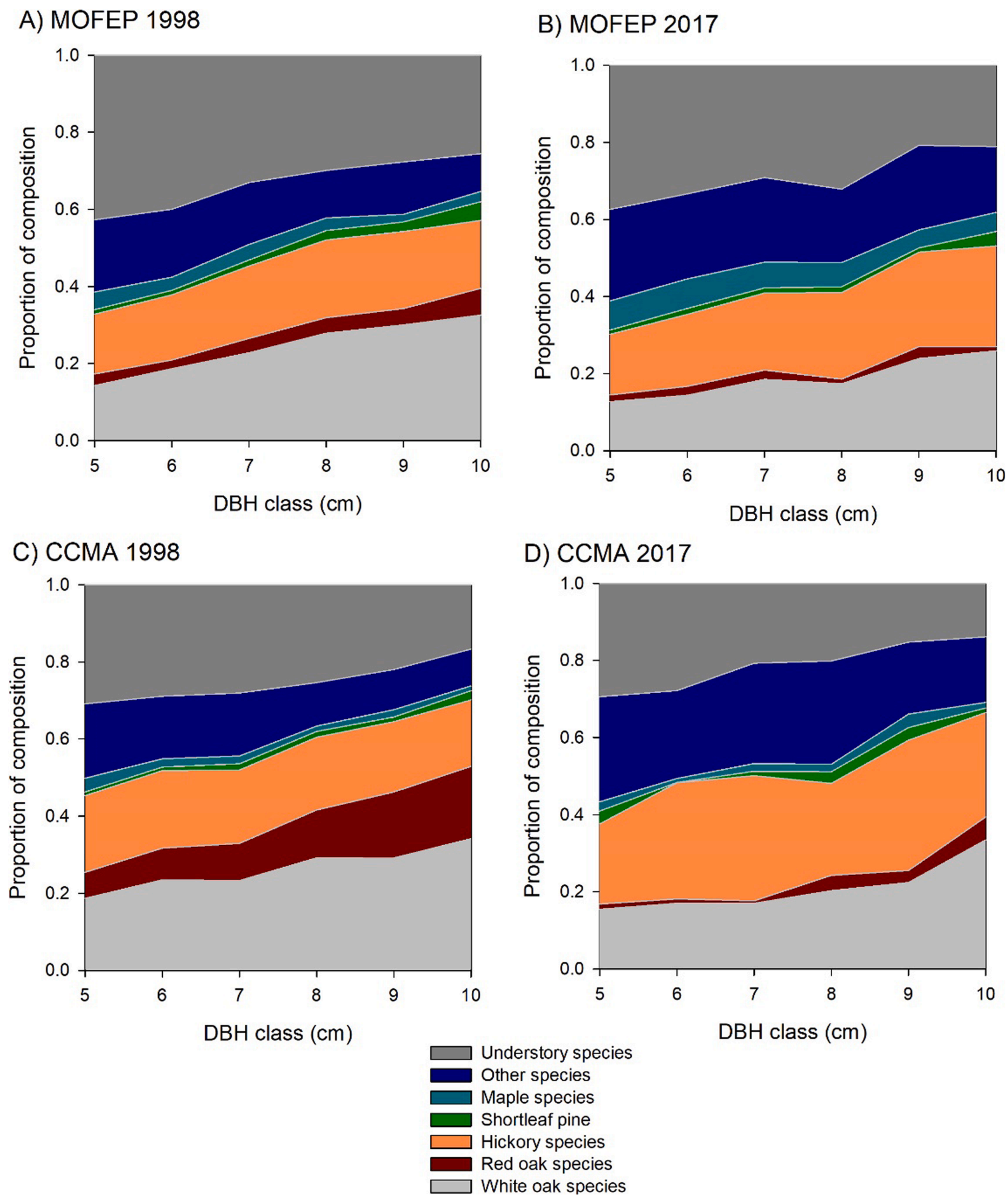

Fig. 10. Proportional abundance of midstory population by species groups by 1-cm diameter classes during the initial sampling period (1998, panels A and C) and the final sampling period (2017, panels B and D) for MOFEP and CCMA, respectively.

4. Discussion

Results from two decades of frequent prescribed burning provide new insights into fire effects on woody structure and tree recruitment in temperate broadleaf ecosystems. Consistent with previous studies (e.g., Waldrop et al., 1992; Arthur et al., 2015; Knapp et al., 2017), top-kill or mortality occurred most readily on small trees. In restoration scenarios, one objective for introducing frequent prescribed burning is to reduce the abundance of midstory stems to create and maintain the open vertical structure of woodlands or savannas (Hutchinson et al., 2005; Vander Yacht et al., 2017; Bassett et al., 2020). However, the 'fire trap' that maintains the open structure also creates a tree recruitment bottleneck (Prior et al., 2010), with long-term effects on the age structure and dynamics of ecosystem development.

Our results show the temporal dynamics at which the reintroduction of frequent fire affects tree recruitment processes. The long period of fire exclusion that occurred in much of the eastern US provided opportunity for the development of abundant woody stems in the understory and midstory layers (Hanberry et al., 2014). As a consequence, transitioning from a recently unburned ecosystem towards open savanna or woodland structure also takes time (Dey et al., 2017; Knapp et al., 2017). Single fires have limited impacts on larger stems, but the accumulated effect of repeated burns result in both more and larger trees being killed or top-killed by fire (Dey and Hartman, 2005; Hutchinson et al. 2012). In our study, the tree recruitment that occurred in the first sampling interval following initiation of fire at CCMA was greater than that observed at unburned MOFEP, perhaps due to the lower mean stand basal area at CCMA when the study began. Although burning in the first sampling interval reduced abundance of the smallest trees (the 5-cm dbh class of the midstory) by nearly half, the abundance of the largest trees in the midstory was not greatly affected. As a result, there was a time lag for impacts on reducing tree recruitment, culminating in recruitment rates of approximately 25% of that observed in the unburned landscape during the final sampling interval.

The observed time lag was related to temporal dynamics in which repeated burning reduced tree abundance in the midstory. The midstory serves as the source population for recruitment, or the population of trees available to grow into the overstory size class. In uneven-aged silvicultural systems, it is often favorable to have diameter distributions with greater numbers of trees in small diameter classes to maintain sustainable numbers of trees to grow into larger diameter classes (Guldin and Baker, 1998; Loewenstein et al., 2000; O'Hara and Gersonde, 2004). While a balanced diameter distribution is likely not needed to sustain the open structure of woodland ecosystems through time, studies of frequently burned, old-growth longleaf pine woodlands have reported rotated sigmoid or reverse-j diameter distributions (Platt et al., 1988; Varner et al., 2003). Following two decades of prescribed burning in our study, the diameter distribution within the midstory layer was essentially uniform (with low abundance), suggesting that tree recruitment will remain low or further reduce in the future. A nearby study found that prescribed burning every four years for over six decades eliminated all trees in the 6–12 cm dbh range, stopping tree recruitment and relegating small-diameter trees to sprouts in the understory (Knapp et al., 2015). We found that midstory tree abundance was more strongly related to tree recruitment as the midstory population was reduced through time by burning (Hypothesis 4), indicating the importance of the midstory population for sustaining recruitment. However, our results also show that the midstory population was not completely eliminated through the end of the study period, a result that does not fully support Hypothesis 5. Episodic tree recruitment may still occur if midstory trees continue to grow into larger size classes.

Frequent prescribed burning at CCMA suppressed tree recruitment rates across a range of stand density levels, including relatively open stands (Hypothesis 3). Relationships between stand density and growing space availability indicate that regeneration and recruitment of new trees is unlikely in dense stands because growing space is occupied by existing trees (Williams, 2003; Loewenstein, 2005). In upland hardwood ecosystems of the study region, basal areas of approximately 14–18 m^2/ha are considered a guideline threshold for full growing space occupancy (Gingrich, 1967). The stand density level associated with full growing space occupancy (i.e., canopy closure) has also been used as a breakpoint in the categorization of "open" and "closed" woodlands, providing a structural target for woodland restoration (Dey et al., 2017). Because frequent prescribed burning alone can take many decades to reduce stand density, management recommendations commonly include thinning in conjunction with prescribed burning for restoring open forest ecosystems (Dey et al., 2017; Knapp et al., 2017; Bassett et al., 2020; Bragg et al., 2020). Creating more open stand conditions is expected to increase the rate of tree recruitment, providing more opportunities for trees to escape the 'fire trap' through more rapid growth (Hoffmann et al., 2020). However, low intensity surface fires have also been reported to reduce growth rates of residual trees (Ford et al., 2010; Refsland et al., 2020), indicating additional research is needed to quantify if growth reductions due to frequent fire may further dampen recruitment rates.

Our results support that frequent prescribed fire reduced tree recruitment through time, but offered limited evidence of shifting species composition in the recruitment or midstory populations (Hypothesis 1). Traits that reduce vulnerability to top-kill or mortality are common in fire-tolerant tree species (Kane et al., 2008; Pellegrini et al., 2017; Nolan et al., 2020) and can contribute to changes in species abundance following fire (Green et al., 2010; Fan et al., 2012). In the eastern US, fire may be prescribed for increasing the relative abundance or dominance of oak species in upland sites (Brose et al., 1999; Arthur et al., 2012; Brose et al., 2013). However, we found no evidence that fire increased the abundance of oaks in the recruitment or midstory population during the course of the study; in contrast, the relative abundance of the red oak group generally decreased through time on both the burned and unburned sites while the relative abundance of the white oak group remained unchanged. The only species to decrease in relative abundance of the recruiting population at the burned CCMA site but not the unburned MOFEP site was scarlet oak, a species that is sensitive to damage from fire due to its relatively thin bark and poor ability to compartmentalize after damage (Kinkead et al., 2017; Dey and Schweitzer, 2018). Other studies have also reported scarlet oak abundance to be reduced in the understory and midstory layers following repeated prescribed burning (Arthur et al., 1998; Fan et al., 2012).

A large body of research supports the role of surface fire in promoting oak regeneration, although a variety of factors affect the importance of fire for oak regeneration success (e.g., Arthur et al., 2012; Brose et al., 2013; Brose, 2014). Our study sites were located in the western portion of the central/eastern US oak geography, where oak species are particularly dominant (Fei et al., 2011). The region has relatively low site productivity and less competitive pressure from tree species such as red maple, sugar maple, American beech (*Fagus grandifolia*), and tulip-poplar (*Liriodendron tulipifera*), which are commonly problematic mesophytic species in regions further east (Nowacki and Abrams, 2008; McEwan et al., 2011; Brose, 2014). In our study, the recruitment population was dominated by oak species prior to the start of the burning treatments, suggesting that problems with mesophication are less common in this region than other locations. However, mesophytic species have increased in the regeneration layer over recent decades (Olson et al., 2017), and our results show increased relative abundance of blackgum and red maple on unburned sites. While prescribed burning appeared to reduce the recruitment of red maple, the relative abundance of blackgum increased regardless of the burn treatment. The only other species to show numerical increase in relative abundance in the recruitment population in the burned sites was pignut hickory. Commonly lumped with oak species, hickory species have unique ecologies that warrant more study, with recent research suggesting increased presence of hickories in oak-hickory forests (Pile Knapp et al., 2021).

While research on fire effects on tree regeneration often focuses on seedling and sapling populations, successful canopy recruitment also requires long-term tree survival. Trees often require decades to transition from the midstory to canopy positions, particularly under the presence of overstory trees (Hart et al., 2012). Accumulated effects of frequent fire increase the likelihood of mortality of hardwood trees, particularly for more fire-sensitive species (Huddle and Pallardy, 1996). The likelihood of mortality from fire decreases as tree size increases (Keyser et al., 2018), but more research is required to understand long-term effects of fire on tree longevity for hardwood trees large enough to avoid top-kill but still recruiting to the canopy. Our results show that repeated burning decreased the probability of survival during the 15-year period after the first recruitment interval, although we found no significant effects of fire on survival within species groups (Hypothesis 3). Studies on effects of long-term, repeated prescribed burning have reported an absence of hardwood trees smaller than around 12 cm dbh after decades of burning (Waldrop et al., 1992; Arthur et al., 2015; Knapp et al., 2015), suggesting a general size threshold for persistence through consistent, repeated burning. Because the defining size for tree recruitment in our study was similar to this size threshold, we expect that the probability of survival for newly recruited trees would be further reduced with additional burning through time, raising questions as to whether new recruits observed in our study would ever make it to the upper canopy without a break in the fire interval.

We found no evidence that the effects of frequent prescribed burning on tree recruitment varied by site type (Hypothesis 2). Variation in site conditions related to aspect and slope position can affect fire behavior across the landscape (Alexander et al., 2006; Holden et al., 2009; Birch et al., 2015). In southeastern Ohio, for example, Iverson et al. (2004) found that fire intensity was related to an index of site moisture derived from topo-edaphic information. In our study, the waterways and protected backslopes were expected to be wetter sites than the summits and exposed backslopes, but the rate at which tree recruitment was reduced through time did not differ among the sites types. Previous research from the region has shown little evidence of topographic effects on fuel characteristics in the region. Deciduous leaf litter, the primary driver of surface fire behavior in the region, is more strongly related to intra-annual temporal variation than to topography (Stambaugh et al., 2011), and similar levels of fuels consumption have been reported across topographic positions following prescribed burning (Kolaks et al., 2004). Although recent research shows that ground flora vegetation responses to prescribed burning varied across site types at CCMA (Maginel et al., 2019), variation in fire behavior across the landscape has not been quantified.

Variation in fire behavior may provide local opportunities for tree recruitment to occur with frequent burning (Hoffmann et al., 2020). While we found no differences in the effect of fire on tree recruitment patterns across ecological site types, our study was not designed to test effects of more local variation on tree recruitment. The persistence of a low number of trees across all size classes within the midstory after two decades of burning might be attributed to local variation in fire behavior. This topic warrants additional research in hardwood forests of this region, as it is unclear if drivers of local variability in fire behavior are spatially random through time or associated with micro-site conditions that would affect the spatial pattern of recruitment over long timescales.

Prescriptions of frequent burning without interruption do not conform to temporal patterns of fire frequency from fire history studies in temperate broadleaf ecosystems of the region, which commonly document important variability in fire return intervals (Batek et al., 1999; Guyette et al., 2002; Stambaugh et al., 2018). Prior to Euro-American settlement, fire return intervals included fire-free periods that could last for decades (Guyette et al., 2002), providing opportunity for regeneration and recruitment events in broadleaf ecosystems (Dey et al., 2017). In open forest ecosystems, increasing fire frequency is associated with maintaining more open conditions associated with savannas relative to open woodlands or closed woodlands (Hanberry et al., 2018). Therefore, frequent and invariable burn prescriptions are not universally appropriate for long-term maintenance across the variety of natural communities of temperate broadleaf open ecosystems.

Effects of frequent prescribed burning have important, long-term implications for developing age structure. In practice, frequent fire is often prescribed to restore open structure, with the intention of removing midstory stems, often without initial interest in tree regeneration and recruitment. However, without providing opportunity for tree recruitment to occur, hardwood ecosystems may maintain or be forced towards even-aged structure. Rather than expecting continuous recruitment to occur with consistent frequent burning, episodic recruitment events may be planned through fire-free intervals that allow small trees to advance from the midstory into size classes resistant to top-kill or mortality (Kabrick et al., 2014; Hanberry et al., 2018; Bragg et al., 2020). Fire-free intervals of several decades have been recommended for oak recruitment (Arthur et al., 2012), during which time the open structure of the ecosystem would temporarily fill in with trees. Explicit consideration of this regeneration phase may be important in management of open oak woodlands and can be incorporated into a management schedule that varies its timing across the landscape to create a mosaic of woodlands in open or regeneration phases across the landscape (Kabrick et al., 2014).

5. Conclusion

Our study highlights three key factors affecting tree recruitment patterns with frequent fire: 1) the presence of a 'source population' of seedlings or saplings; 2) sustained growth to transition small trees into larger size classes; 3) avoidance of top-kill or mortality of new recruits with continued burning. Through time, repeated fire depletes the source population of midstory trees, particularly in the smallest size class. By the end of our study period, however, a low number of trees persisted across all midstory size classes, indicating that the source population had not been fully eliminated. Maintaining recruitment through time thus requires sustained growth of these trees at rates sufficient to eventually reach a size resistant to top-kill. However, ingrowth also decreased with increasing overstory density, as overstory density suppresses growth and lengthens the time that midstory trees remain small and vulnerable to top-kill or mortality. Frequent burning reduced tree recruitment for all tree species and did not appear to cause a shift to fire-tolerant species. The magnitude of tree recruitment reduction was similar regardless of site type. Overall, there was little evidence of continuous tree recruitment occurring under a frequent prescribed burning regime, demonstrating that a fire-free interval is necessary for tree recruitment to occur, even in open oak woodlands that are generally considered fire dependent.

CRediT authorship contribution statement

Benjamin O. Knapp: Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Calvin J. Maginel:** Conceptualization, Methodology, Writing – review & editing. **Bradley Graham:** Writing – review & editing, Project administration. **John M. Kabrick:** Conceptualization, Methodology, Writing – review & editing. **Daniel C. Dey:** Conceptualization, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120191.

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