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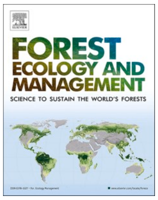

Fire exclusion vs. a fire-free interval following repeated prescribed fire: Consequences for forest stand structure and species composition in an upland oak forest

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ABSTRACT

In the Central Appalachian forest region, oaks (*Quercus* L.) and other disturbance-dependent tree species are experiencing widespread regeneration failure after decades of fire suppression. Managers use prescribed fire to decrease basal area with the aim of facilitating oak regeneration and shifting species composition toward pyrophytic species that dominate the overstory. Although fire may set the stage for improved oak regeneration, a fire-free period is necessary for oak seedlings to develop into fire-resistant stems. The effects of prescribed fire have been amply investigated across the region, but few studies have examined changes to stand structure and oak regeneration after cessation of burning. We followed the effects of three treatments, fire-excluded, 3x-burned, and 4x-burned, for 20 years. After a fire-free interval of approximately ten years, burned treatments had significantly lower total basal area and greater relative density of oaks in the subcanopy (10–20 cm DBH) than the fire-excluded treatment. The 4x-burned, which had the greatest reduction in basal area, also had greater relative density of midstory oaks (2–10 cm DBH), and higher stem density of oak regeneration (<2 cm DBH) than the fire-excluded. Despite these trends towards increased regeneration of oaks and other pyrophytes, red maple (*Acer rubrum* L.) stem density also increased in the midstory of burned treatments, suggesting a legacy effect of decades of fire suppression and the concomitant mesophication that has occurred. We also examined the effects of continued fire exclusion on the fire-excluded reference treatment. Additional evidence of mesophication on this treatment was demonstrated by increased overstory (≥20 cm DBH) and subcanopy red maple stem density as well as midstory (2–10 cm DBH) eastern white pine (*Pinus strobus* L.) stem density, a prominent mesophyte on these sites. This study supports the idea that repeated prescribed burning followed by a 10-year fire-free interval can alter stand structure and lead to improved oak regeneration by increasing canopy openness. However, the results were variable across burned treatments (3x vs. 4x) and the ingrowth of red maple and other mesophytes after only 10 years of fire exclusion will require additional control measures. Successful maintenance of oak-dominated forests on upland sites in the Central Appalachian hardwoods region may be contingent on a subsequent canopy disturbance that further increases light availability followed by a fire-free interval. Importantly, in the absence of burning or other disturbance, red maple and other mesophytic species will continue to increase in relative stem density.

1. Introduction

Forested landscapes of the Central Appalachians were shaped for millennia by shifting climate, changing vegetation, and the long-term and highly varied use of fire by Native Americans over 11,000 years, and much more recently, by Euro-American colonizers (Fowler and Konopik, 2007; Lafon et al., 2017; McEwan et al., 2011). In response to increasingly severe, landscape-scale fires across the U.S., fire suppression policies and tactics were established in the early 20th century, leading to the near-cessation of fires across the Central Appalachians (Arthur et al., 2021) in a landscape for which the historic median fire return interval was estimated to be 5.4 years (Lafon et al., 2017). As a

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result, forest ecosystems in this region have been essentially without fire for 80–100 years, with significant consequences for both species composition (Brose et al., 2014; Nowacki and Abrams, 2008), and depth and composition of the fuel bed and associated forest floor communities (Carpenter et al., 2020). The absence of fire in these forest ecosystems for 50–100 years is recognized as a key cause of oak regeneration failures across the Central Hardwood and Appalachian regions (Dey and Schweitzer, 2015). Despite the increasingly apparent importance of fire as a disturbance agent in these ecosystems and the use of prescribed fire as a management tool, the role of fire in this region is still understudied (Varner et al., 2016). In particular, there is a paucity of information regarding how a fire-free period following management with prescribed fire can be used to promote oak (*Quercus* spp. L.) and other pyrophytic species such as the hard pines (*Pinus* subgenus *Pinus*) in upland forests historically dominated by these species but increasingly dominated by mesophytic species (Nowacki and Abrams, 2008).

Oaks are a foundational genus in the eastern United States (Hanberry and Nowacki, 2016), and continued oak dominance is threatened by the lack of landscape scale disturbance (Fei et al., 2011; Nowacki and Abrams, 2015). In the Central Appalachians, upland oak species, on these sites including, but not limited to, chestnut oak (*Quercus montana* Willd.), white oak (*Q. alba* L.), scarlet oak (*Q. coccinea* Muenchh.) and black oak (*Q. velutina* Lam.), have low to intermediate shade tolerance (Burns and Honkala, 1990). As such, they cannot successfully compete in the increasingly dense and shady forest understories that develop in the absence of disturbances, such as occurs with fire suppression (Hanberry et al., 2020a; Nowacki and Abrams, 2008). Further evidence of the importance of fire to maintaining oak dominance in these forests, oaks as a group have a suite of fire-adaptive traits, including sprouting, litter flammability, and bark allometry (Arthur et al., 2021; Babl et al., 2020, Varner et al., 2016). Taken together, we understand that fire disturbance in the past has likely contributed to the creation and maintenance of conditions, such as canopy openness, that support oak dominance (Abrams, 1996). As a result, researchers have posited that when the canopy is sufficiently open and fire cessation lasts long enough for oak seedlings to grow large enough to resist future fire, prescribed burning should facilitate oak establishment (Arthur et al., 2012).

It is now well understood that single prescribed fires have little to no direct effect on overstory stem densities, and that repeated fire or additional treatments such as mechanical thinning or herbiciding may be needed to influence the structure and composition in many stands not burned for decades (Arthur et al., 2021). Repeated burning reduces sapling and midstory stem density (Arthur et al., 2015; Blankenship and Arthur, 2006; Brose et al., 2013) and can also reduce density of subcanopy stems 10–20 cm DBH (Arthur et al., 2015; Hutchinson et al., 2012b). However, fire can lead to increased sprouting of mesophytic species, which can remain competitive with oaks (Blankenship and Arthur, 2006; Green et al., 2010). Repeated burning may also limit oak recruitment by killing small oak stems before they are large enough to resist fire and be recruited to the canopy (Blankenship and Arthur, 2006; Knapp et al., 2015; Knapp et al., 2017). A major canopy disturbance after repeated burning provides the most benefit to oak regeneration by increasing light availability (Arthur et al., 2012; Brose, 2014; Hutchinson et al., 2012b; Johnson et al., 2019). As natural disturbance is unpredictable and mechanical manipulation not always possible, e.g., where harvesting is restricted or cost-prohibitive, prescribed fire may be the only tool available to facilitate oak regeneration. Researchers have called for a fire-free interval of more than four years (Knapp et al., 2017) and up to 10 to 30 years (Arthur et al., 2012; Dey and Schweitzer, 2015) to allow oak seedlings to establish and grow large enough to resist future fire (Arthur et al., 2012; Knapp et al., 2015; Knapp et al., 2017). This study provided the opportunity to test whether a 10-year fire-free interval after repeated burning produced the hypothesized conditions for oaks to recruit into the sapling and midstory size-classes in stands that experienced long-term fire suppression, and/or whether the legacy effects of fire suppression complicate this dynamic.

An investigation of the effects of prescribed fire on forest structure and species composition was initiated in 1995 in collaboration with the USDA Forest Service in the Daniel Boone National Forest (DBNF), Kentucky. Multiple studies elucidating the short- and mid-term responses to single (Blankenship and Arthur, 1999a, 1999b; Gilbert et al., 2003; Kuddes-Fischer and Arthur, 2002) and repeated fires (Arthur et al., 1998, Blankenship and Arthur, 2006; Chiang et al., 2005; Green et al., 2010) developed from this ongoing investigation. This study builds on this previous research to examine the effects of a 10-year fire-free interval on changes in stand structure and species composition, taking advantage of permanent plots established in 1995 in the Red River Gorge Geological Area within the DBNF.

We hypothesized that after a 10-year fire-free interval following previous repeated burning, basal area and stem density would be reduced overall on burned treatments compared to pre-burn and to fire-excluded (H1). Because oaks and other pyrophytic species require more light to regenerate (Johnson et al. 2019), we also hypothesized that, if H1 is supported, the density of oaks and other pyrophytes in the regeneration and midstory size-classes would increase relative to red maple and other mesophytic species compared to pre-burn and post-burn measurements, and compared to the fire-excluded treatment (H2). On this study site, oaks are the dominant pyrophyte, followed by the hard pines as a group; red maple (*Acer rubrum* L.), and eastern white pine (*Pinus strobus* L.) secondarily, are the dominant mesophytes. We further hypothesized that continued fire-exclusion on the fire-excluded treatment would allow red maple and other mesophytic species to grow into the subcanopy and overstory (≥10 cm DBH) during the fire-free interval, significantly increasing in density (H3).

2. Methods

2.1. Site description

Three non-conterminous ridges were selected initially as replicates in the Cumberland Ranger District of the Daniel Boone National Forest, in the Red River Gorge Geological Area, located within the Cliff Section of the Cumberland Plateau (Braun, 1950). Over the two decades of research, we dropped one of the three ridges as a study site due to impacts of hiking and camping in the area, leaving two study sites, Whittleton Ridge and Klaber Ridge. The geological substrate of the sites are shales and siltstones of the Upper and Lower members of the Lee formation (Weir and Richards, 1974). Klaber Ridge soils are classified as Latham-Shelocta silt loams that are moderately deep and well drained, slowly permeable clayey soils of the subgroups Typic and Aquic Hapludults (Avers et al., 1974). Whittleton Ridge soils are classified as Gilpin silt loam, which is moderately deep and well drained, with a lower subsoil of silty clay loam of the subgroup Typic Hapludult (Hayes, 1993). Mean annual precipitation is 130 cm, with a mean growing season of 176 days. Mean annual temperature is 12 °C, with mean daily temperatures ranging from 0 °C in January to 31 °C in July (Foster and Conner, 2001).

The sites are mature, second-growth forests dominated by chestnut oak and scarlet oak, with black oak, white oak, and hickories (*Carya* spp. Nutt.) frequently present. Pitch pine (*Pinus rigida* Mill.), shortleaf pine (*P. echinata* Mill.), and Virginia pine (*P. virginiana* Mill.) are common in the overstory. The subcanopy and midstory are dominated by red maple, eastern white pine, blackgum (*Nyssa sylvatica* Marsh.), and sourwood (*Oxydendrum arboreum* L.). This area was established as the Cumberland National Forest in 1937; the forest condition of this area was described at that time as “cutover” or “heavily culled” (Collins, 1975), and there has been no management on the sites for at least 35 years prior to the start of the study (Blankenship and Arthur, 2006). The Red River Gorge Geological Area is an intensively used recreational area, and as such, has very low deer herbivory pressure. As of 2016, the overstory oaks were approximately 80 years old and red maples were approximately 60 years old (Washburn and Arthur, 2003).

2.2. Experimental design and fire application

Whittleton and Klaber Ridges each had three treatment units: a fire-excluded reference and two units with different burn frequencies, with prescribed fire applied to the burned units periodically in an adaptive management approach in collaboration with USDA Forest Service personnel. As of 2016, treatment units on both ridges included a fire-excluded unit, a 3x-burned unit, and a 4x-burned unit. For burn conditions and timing see Green et al. (2010). Prescribed fire was last implemented on Klaber Ridge in 2004 and on Whittleton Ridge in 2005.

Forest Service personnel performed all prescribed burns using drip torch ignition. Firing began from the highest points on the ridges and was pulled downslope from the ridges into the wind, burning across the whole treatment area. Strip-firing and point-source were used if backing fires were not sufficiently intense (>0.3 m flame length; Richardson, 1995). Fires from 1995 through 2000 were performed between March 13 and 31; fires after 2000 were conducted in April in recognition of a need for early growing season burning to further control competing woody vegetation. All fires were low intensity surface fires with flame lengths between 0.3 m and 2 m [see Green et al. (2010) for all fire behavior and burn condition information].

In 1995, eight permanent 500 m^2 circular plots were established in each treatment unit resulting in 48 plots across the two study ridges. Since then, recreational impacts from hiking and camping as well as wildfires from escaped campfires led to the loss of 2 plots in the 4x-burned unit and 5 plots in the 3x-burned unit of Klaber Ridge, for a total sample size of 41 plots across the two ridges at the time of last sampling in 2015.

2.3. Data collection and analysis

Plots were sampled in 1995 prior to burning and then intermittently, most recently in July and August of 2015. Data were collected in the same manner as in Blankenship and Arthur (2006). For all stems $\geq$ 2 cm diameter at breast height (DBH), the DBH, and species were recorded. Stems < 2 cm DBH were tallied by species in a circular 25 m^2 area centered about the original plot center.

We analyzed data collected before treatment (1995), 1 to 2 years after cessation of burning (2007), and after a fire-free period (2015) to assess changes in stem density and basal area for all stems and select species and species groups. For the analyses in this paper, we grouped stems into overstory ($\geq$20 cm DBH), subcanopy (10–20 cm DBH), midstory (2–10 cm DBH), and regeneration (<2 cm DBH) size-classes. These categories were based upon previous literature that reported that prescribed fire differentially affects stems of different diameters with low mortality of stems $\geq$ 20 cm DBH (Arthur et al., 2015; Blankenship and Arthur, 2006; Hutchinson et al., 2005). For stems < 2 cm DBH, we analyzed stem density for all stems and select species and species groups in 1995, 2003 and in 2015. We used data from 2003 (before the last burn) because regeneration data were not collected in 2007 (after burning). Therefore, to determine whether an additional burn followed by an extended fire-free period increased oak recruitment into the midstory, we were limited to analyzing changes from 2003 to 2015.

Total stem density and stem density by species or species group were analyzed for each size-class when data were sufficient for analysis (i.e., lacking an abundance of zero counts). Species or species groups analyzed included the pyrophytes - oak, hickory and hard pines, and the mesophytes - red maple, sourwood, eastern white pine and blackgum (classifications *sensu* Arthur et al., 2021; Saladyga et al., 2022). For simplification, we lumped Virginia pine, often categorized as intermediate, with the other hard pines; we included blackgum, also categorized as intermediate, as a mesophyte.

For statistical analysis, a repeated measures ANOVA was utilized in the linear mixed model framework including treatment, year, site, and treatment*year as fixed factors using PROC GLIMMIX in SAS™ Statistical Software (SAS, 2011). Data were transformed using log(y) or square root(y) when necessary to meet ANOVA assumptions of normality. An unstructured covariance was used to model correlation between plots. When there was a significant treatment effect or treatment by year interaction (determined at $\alpha = 0.05$), post-hoc pairwise comparisons were made. Results were considered significant at $p < 0.05$, and marginally significant for p-values between 0.05 and 0.10.

3. Results

3.1. Changes in stand structure

We hypothesized that after a 10-year fire-free interval following repeated prescribed fire, total basal area and stem density would decline on both burned treatments compared to pre-burn and compared to the fire-excluded treatment (H1). This hypothesis was partially supported. Total basal area significantly decreased on the 4x-burned from 1995 to 2007 ($p = 0.0311$) and from 2007 to 2015 ($p = 0.0239$) but did not change on the 3x-burned (1995–2007: $p = 0.329$; 2007–2015: $p = 0.808$) or on the fire-excluded (1995–2007: $p = 0.656$; 2007–2015: $p = 0.534$; Table 1). Before burning, the 3x-burned had significantly lower total basal area than the other treatments (FE: $p = 0.0329$; 4x: $p = 0.0146$). In 2015, total basal area was lowest on the 4x-burned and highest in the fire-excluded (Table 1).

Significant decreases in total stem density occurred between 1995 and 2007 on both burned treatments ($p < 0.0001$ for 3x and 4x; $p = 0.155$ for FE; Table 1). In 2007, total density on the fire-excluded was significantly greater than either of the burned treatments (3x: $p = 0.0006$; 4x: $p < 0.0001$), but during the fire-free interval, from 2007 to 2015, total stem density increased significantly on the 4x-burned ($p < 0.0001$), entirely in the midstory size-class. In 2015, total density on the 4x-burned was significantly greater than the 3x-burned ($p = 0.0003$) and the fire-excluded ($p = 0.0235$; Table 1). We examined changes to stem density and basal within each size-class to discern where changes were occurring.

Overstory structure changed throughout the study, primarily on the 4x-burned treatment. Before implementation of prescribed fire to the study sites in 1995, overstory stem density and basal area were statistically similar among the three treatments (Table 1) and remained similar among the treatments in 2007 after three and four prescribed fires. Total overstory stem density decreased significantly from 1995 to 2015 on the 4x-burned ($p = 0.0276$), and did not change on either the fire-excluded ($p = 0.576$) or the 3x-burned ($p = 0.264$; Table 1). By 2015, after a 10-year fire-free interval, overstory stem density was lower on the 4x-burned than on the 3x-burned ($p = 0.0482$) and marginally significantly lower than the fire-excluded ($p = 0.0668$). Overstory basal area in 2015 on the 4x-burned was also significantly lower than on the fire-excluded ($p = 0.0020$), and marginally significantly lower than on the 3x-burned ($p = 0.0774$).

In the subcanopy (10–20 cm DBH), burning significantly reduced total stem density and basal area, and remained lower on the burned treatments compared to the fire-excluded (Table 1). Stem density decreased on burned treatments from 1995 to 2007 (3x: $p = 0.00254$; 4x: $p = 0.0048$) and from 2007 to 2015 (3x: $p < 0.0001$; 4x: $p = 0.0107$), as did basal area (1995–2007, 3x: $p = 0.0794$; 4x: $p = 0.0067$; 2007–2015, 3x: $p = 0.0007$; 4x: $p = 0.0048$). Burned treatments had significantly lower subcanopy stem density and basal area than the fire-excluded in 2007 (SD 3x: $p = 0.0103$, 4x: $p < 0.0001$; BA 3x: $p = 0.0334$, 4x: $p < 0.0001$) and in 2015 (SD 3x: $p < 0.0001$, 4x: $p < 0.0001$; BA 3x: $p = 0.0005$, 4x: $p < 0.0001$; Table 1). In addition, the 4x-burned treatment had significantly lower subcanopy stem density and basal area than the 3x-burned in 2007 (SD: $p = 0.0046$; BA: $p = 0.0144$) and in 2015 (SD: $p = 0.0282$; BA: $p = 0.0312$).

Midstory (2–10 cm DBH) stem density and basal area were also reduced by burning, but rebounded during the fire-free period. Between 1995 and 2007, midstory stem density decreased on all treatments, but

Table 1

Mean stem density (stems ha^{-1}) and mean basal area (m^2 ha^{-1}) for all size-classes on all treatments prior to burning in 1995, after fire (2007), and after a fire-free interval (2015) on study sites in the Daniel Boone National Forest, Kentucky. Values in parentheses represent standard error. Different uppercase superscript letters indicate significant differences among treatments for the same year and different lowercase superscript letters indicate significant differences among sampling dates within a treatment at α = 0.05. No superscripts present where differences were not significant.

	Density (stems ha^{-1})			Basal Area (m^2 ha^{-1})		
Treatment	1995	2007	2015	1995	2007	2015
Total						
Fire-excluded	1844 (126)^{a}	1381 (78)^{Aab}	1255 (73)^{Ab}	32.3 (2.9)^{A}	30.8 (1.5)	31.8 (1.2)^{A}
3x-burned	1977 (132)^{a}	555 (37)^{Bb}	988 (144)^{Ab}	24.7 (2.6)^{B}	26.5 (1.6)	26.5 (1.5)^{B}
4x-burned	2267 (114)^{a}	375 (33)^{Bb}	1844 (276)^{Ba}	33.6 (2.8)^{Aa}	25.1 (2.7)^{b}	22.7 (1.7)^{Cc}
Overstory (≥20 cm DBH)						
Fire-excluded	262 (40)	244 (15)	244 (14)^{AB}	23.6 (3.0)	24.1 (1.5)	25.7 (1.3)^{A}
3x-burned	218 (35)	251 (16)	262 (19)^{A}	15.7 (2.6)^{a}	22.9 (1.4)^{b}	23.8 (1.5)^{ABb}
4x-burned	286 (35)^{ab}	234 (28)^{a}	201 (22)^{Bb}	24.0 (3.2)^{a}	22.9 (2.5)^{a}	19.9 (1.9)^{Bb}
Subcanopy (10–20 cm DBH)						
Fire-excluded	338 (46)	304 (21)^{A}	280 (23)^{A}	5.81 (1.0)	4.86 (0.29)^{A}	4.61 (0.37)^{A}
3x-burned	355 (41)^{a}	209 (32)^{Bb}	136 (19)^{Bc}	5.76 (0.95)^{a}	3.20 (0.50)^{Ba}	2.29 (0.39)^{Bb}
4x-burned	350 (56)^{a}	109 (17)^{Cb}	73 (12)^{Cc}	5.43 (1.0)^{a}	2.13 (0.34)^{Cb}	1.57 (0.26)^{Cc}
Midstory (2–10 cm DBH)						
Fire-excluded	1244 (139)^{Aa}	834 (77)^{Ab}	729 (69)^{Ab}	2.93 (0.37)^{a}	1.86 (0.18)^{Ab}	1.58 (0.16)^{Ab}
3x-burned	1355 (142)^{ABa}	104 (25)^{Bb}	467 (125)^{Ac}	3.30 (0.45)^{a}	0.336 (0.65)^{Bb}	0.426 (0.09)^{Bb}
4x-burned	1621 (100)^{Ba}	47 (16)^{Cb}	1624 (307)^{Ba}	4.17 (0.38)^{a}	0.087 (0.04)^{Bb}	1.24 (0.26)^{Aa}

more stems died on the prescribed fire treatments than on the fire-excluded treatment (4x: 97%, 3x: 92%, FE: 33%; $p < 0.0001$; Table 1) and remained higher on the fire-excluded treatment than on both burned treatments. During the fire-free period from 2007 to 2015, midstory stem density increased significantly on the burned treatments ($p < 0.0001$ for both). This increase was especially dramatic on the 4x-burned, which had significantly higher midstory stem density than the 3x-burned ($p < 0.0001$) and the fire-excluded ($p = 0.0015$).

3.2. Shifts in species abundance of pyrophytes vs. mesophytes

In anticipation of finding reduced basal area on the burned treatments, we hypothesized that the higher light availability afforded by lower stem density and basal area would lead to greater density of oaks and other pyrophytes in the regeneration and midstory size-classes. We found that species composition differed among treatments in all size-classes and shifted throughout the study. For this analysis, we examined all size-classes, although the focus of H2 was on the recruitment of oaks and hard pines to the midstory relative to red maple and other mesophytes, and the density of these species in the regeneration size-class.

3.2.1. Oaks and other pyrophytes

Overstory oak stem density and basal area did not change from 1995 to 2007 on any treatment, but decreases occurred on the 4x-burned during the fire-free interval. By 2015, overstory oak stem density and basal area had decreased significantly on the 4x-burned (SD: $p = 0.0016$, Fig. 1A; BA: $p = 0.016$), and oak basal area was significantly lower than on the fire-excluded ($p = 0.026$). Burned treatments did not differ significantly from each other in 2015 (SD: $p = 0.142$; BA: $p = 0.181$) due to high variability among plots. Relative density of oaks in the overstory on the 4x-burned also decreased significantly from 2007 to 2015 ($p = 0.0053$; Table 2). Relative density of overstory oaks also declined on the 3x-burned, but the change was not statistically significant ($p = 0.740$; Table 2).

In the subcanopy, oak stem density and basal area decreased across all treatments (Fig. 1B). However, the relative density of subcanopy oaks on burned treatments increased compared to that on the fire-excluded during the fire-free period (Table 3). Subcanopy oak basal area decreased significantly from 1995 to 2007 on the fire-excluded (2.51 to 0.909 m^2 ha^{-1}, $p = 0.0374$) and the 3x-burned (3.53 to 1.69 m^2 ha^{-1}, $p = 0.046$). After the fire-free period, subcanopy oak stem density decreased significantly on all treatments (FE: $p = 0.0095$, 3x: $p = 0.0296$, 4x: $p = 0.0226$; Fig. 1B), although the 3x-burned had significantly more subcanopy oak stems than the fire-excluded (60 vs. 33 stems ha^{-1}, $p = 0.0435$; Fig. 1B); oak stem density on the 4x-burned was similar to that on 3x-burned and fire-excluded. During the same period, subcanopy oak basal area decreased on the 3x-burned (1.69 to 1.29 m^2 ha^{-1}, $p = 0.0067$), the 4x-burned (1.40 to 1.02 m^2 ha^{-1}, $p = 0.005$), and marginally significantly on the fire-excluded (0.909 to 0.676 m^2 ha^{-1}, p

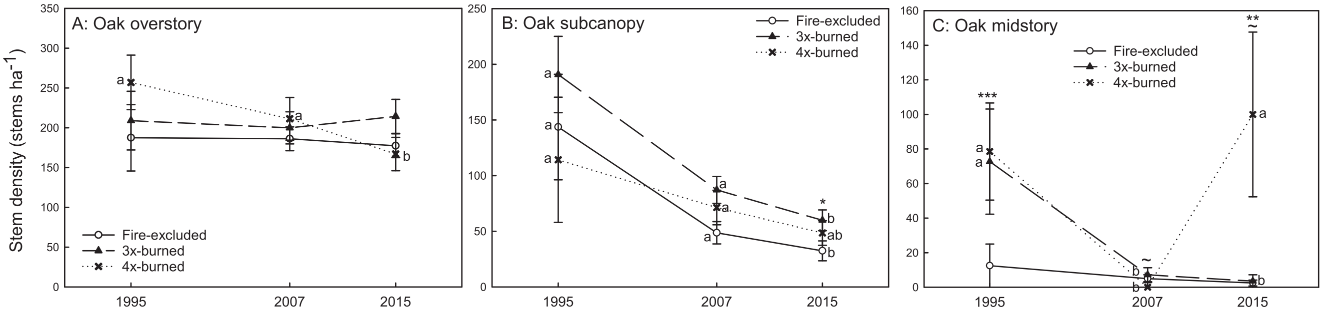

Fig. 1. A) Oak overstory (≥20 cm DBH), B) oak subcanopy (10–20 cm DBH), and C) oak midstory (2–10 cm DBH) stem density (stems ha^{-1}) for size-classes for all treatments before fire (1995), after fire (2007), and after a fire-free interval (2015) on study sites in the Daniel Boone National Forest, Kentucky. Different lowercase letters indicate significant difference between years within a treatment. If no difference between years, then no letters present. Differences among treatments within year are denoted as follows: *** indicates both burned treatments were significantly different from the fire-excluded, ** indicates only the 4x-burned treatment was significantly different from the fire-excluded, * indicates only the 3x-burned treatment was significantly different from the fire-excluded, ~ indicates that the burned treatments were significantly different from each other (α = 0.05). Error bars are ± 1 standard error of the mean.

Table 2

Relative density for overstory (≥20 cm DBH) by species and species groups (%) and total overstory density (stems ha^{-1}) for all treatments prior to burning in 1995, after fire (2007), and after a fire-free interval (2015) on study sites in the Daniel Boone National Forest, Kentucky. Different uppercase superscript letters indicate significant differences among treatments for the same year and different lowercase superscript letters indicate significant differences among sampling dates within a treatment at α = 0.05. No superscripts present where differences were not significant.

Species	Fire-excluded (n = 16)			3x-burned (n = 11)			4x-burned (n = 14)		
	1995	2007	2015	1995	2007	2015	1995	2007	2015
Quercus spp.[1]	71	77^{A}	72	96	85^{A}	82	90^{a}	90^{Ba}	83^{b}
Acer rubrum	4.8^{a}	13^{Ab}	19^{Ac}	0	5.1^{A}	9.0^{B}	2.5	3.7^{B}	7.0^{B}
Carya spp.[2]	2.4	0.5	1.0	0	0.7	0.7	0	0.6	0.7
Nyssa sylvatica	4.8	2.1	2.0	0	0.7	1.4	0	0.6	1.4
Pinus spp.[3]	17	2.6	2.0	4.2	2.2	0.7	5.0	2.4	2.1
Pinus strobus	0	2.6	2.0	0	3.6	4.2	2.5	3.0	2.8
Other spp.[4]	0	1.5	1.5	0	2.8	2.1	0	0	2.8
Total Density (stems ha^{-1})	263	244	244	218	251	262	286	234	201

[1] *Quercus* spp. include *Quercus alba, Q. coccinea, Q. montana,* and *Q. velutina.*

[2] *Carya* sp. include *Carya glabra* and *C. tomentosa.*

[3] *Pinus* spp. include *Pinus echinata, P. rigida* and *P. virginiana.*

[4] Other spp. include *Liriodendron tulipifera, Magnolia acuminata, M. macrophylla, Oxydendrum arboreum, Sassafras albidum,* and *Tsuga canadensis.*

Table 3

Relative density (%) of subcanopy stems (10–20 cm DBH) by species and species groups and total density (stems ha^{-1}) of subcanopy stems prior to burning (1995), after fire (2007), and after a fire free interval (2015) for all treatments on study sites in the Daniel Boone National Forest, Kentucky. Different uppercase superscript letters indicate significant differences among treatments for the same year and different lowercase superscript letters indicate significant differences among sampling dates within a treatment at α = 0.05. No superscripts present where differences were not significant.

Species	Fire-excluded (n = 16)			3x-burned (n = 11)			4x-burned (n = 14)		
	1995	2007	2015	1995	2007	2015	1995	2007	2015
Quercus spp.[1]	43	16^{A}	12^{A}	54	42^{B}	44^{B}	33^{a}	66^{Bb}	67^{Bb}
Acer rubrum	37^{a}	67^{Ab}	67^{Ab}	26	34^{B}	23^{B}	33	13^{B}	14^{B}
Carya spp.[2]	1.9	2.1	2.2	0	0.9	1.3	6.1	3.9	3.9
Nyssa sylvatica	1.9	2.1	2.2	0	7.0	9.3	2.0	2.6	9.8
Oxydendrum arboreum	9.3	3.7	4.4	10	9.6	11	10	3.9	3.9
Pinus spp.[3]	0	0	0	0	0	0	2.0	0	0
Pinus strobus	3.7	6.2	8.0^{A}	2.6	4.3	8.0^{AB}	14^{a}	9.2^{a}	0^{Bb}
Other spp.[4]	3.7	3.3	4.9	7.7	2.6	4.0	0	1.3	2.0
Total Density (stems ha^{-1})	338	304	280	355	209	136	350	109	73

[1] *Quercus* spp. include *Quercus alba, Q. coccinea, Q. montana,* and *Q. velutina.*

[2] *Carya* spp. include *Carya glabra* and *C. tomentosa.*

[3] *Pinus* spp include *Pinus echinata, P. rigida* and *P. virginiana.*

[4] Other spp. include *Liriodendron tulipifera, Magnolia acuminata, M. macrophylla, Sassafras albidum,* and *Tsuga canadensis.*

= 0.0543).

Relative density of subcanopy oak was higher on both burned treatments compared to the fire-excluded in 2007 (3x: $p = 0.0032$; 4x: $p < 0.0001$) and 2015 (3x: $p = 0.0023$; 4x: $p < 0.0001$; Table 3). On the fire-excluded, relative density of subcanopy oak decreased from 43% in 1995 to 16% in 2007, a marginally significant difference ($p = 0.0542$). Conversely, on the 4x-burned, subcanopy oak relative density increased significantly from 33% in 1995 to 66% in 2007 ($p = 0.0484$). On the 3x-burned, relative density of subcanopy oak remained static across years, but was higher than on the fire-excluded (2007: $p = 0.0032$; 2015: $p =$

Table 4

Relative density (%) and total density (stems ha^{-1}) of midstory stems (2–10 cm DBH) prior to burning (1995), after fire (2007), and after a fire-free interval (2015) for all treatments on study sites in the Daniel Boone National Forest, Kentucky. Different uppercase superscript letters indicate significant differences among treatments for the same year and different lowercase superscript letters indicate significant differences among sampling dates within a treatment at α = 0.05. No superscripts present where differences were not significant.

Species	Fire-excluded (n = 16)			3x-burned (n = 11)			4x-burned (n = 14)		
	1995	2007	2015	1995	2007	2015	1995	2007	2015
Quercus spp.[1]	1.0	0.6^{A}	0.2^{A}	5.4^{a}	7.0^{Ba}	0.8^{ABb}	4.8^{a}	0^{Ab}	6.1^{Ba}
Acer rubrum	55	44	35	42	54	64	55^{a}	46^{b}	38^{b}
Carya spp.[2]	0.5	0.7	0.9	0.7	1.8	0.4	1.3	3.0	2.7
Nyssa sylvatica	9.0	14	11	19^{a}	21^{a}	3.5^{b}	13	36	5.5
Oxydendrum arboreum	4.0	2.8^{A}	4.0^{A}	11^{a}	11^{Ba}	28^{Bb}	7.4^{a}	3.0^{Aa}	22^{Bb}
Pinus spp.[3]	0	0	0	0	0	0	0	0	6.0
Pinus strobus	18^{a}	34^{Ab}	42^{Ac}	7.4	1.8^{B}	0^{B}	7.0^{a}	0^{Bb}	0.6^{Bb}
Other spp.[4]	13	4.3	7.6	15	3.5	3.5	12	12	20
Total Density (stems ha^{-1})	1244	834	729	1355	104	467	1621	47	1624

[1] *Quercus* spp. include *Quercus alba, Q. coccinea, Q. montana,* and *Q. velutina.*

[2] *Carya* spp. include *Carya glabra* and *C. tomentosa.*

[3] *Pinus* spp. include *Pinus echinata, P. rigida* and *P. virginiana.*

[4] Other spp. include *Fagus grandifolia, Juniperus virginiana, Liriodendron tulipifera, Magnolia acuminata, M. macrophylla, Sassafras albidum,* and *Tsuga canadensis.*

0.0023) and statistically similar to that on the 4x-burned (2007: $p = 0.374$; 2015: $p = 0.45$).

Midstory oak stem density decreased significantly from 1995 to 2007 after repeated burning on both burned treatments ($p < 0.018$), and then increased dramatically in 2015 on the 4x-burned only ($p < 0.0001$; Fig. 1C). In 2015, relative density of midstory oaks was the highest on the 4x-burned (FE: $p = 0.0072$; 3x: $p = 0.265$). Relative density of midstory oaks was highest on the 3x-burned in 2007 (FE: $p = 0.0059$; 4x: $p = 0.0043$; Table 4) but declined in 2015. Hard pine species in the midstory were recorded only on the 4x-burned in 2015 (93 stems ha^{-1}).

In the regeneration size-class (stems < 2.0 cm DBH), stem densities increased from 1995 to 2003 on all treatments (FE and 4x: $p < 0.0001$; 3x: $p = 0.0029$) and remained similar across treatments in each measurement year (Fig. 2A). Densities of oak and hard pines were similar among treatments in 1995 and 2003, and increased in density throughout the study but more so on the 4x-burned treatment (Fig. 2B and 2C). Between 1995 and 2003, oaks increased on all treatments (FE: $p = 0.0009$; 3x: $p = 0.0201$; 4x: $p = 0.0001$), and hard pines increased on the fire-excluded ($p = 0.0095$) and the 4x-burned ($p = 0.0047$). From 2003 to 2015, regeneration increased on the 4x-burned for oak ($p = 0.0032$) and hard pines ($p < 0.0001$). Hard pine regeneration also increased from 2003 to 2015 on the 3x-burned ($p = 0.0461$) but decreased significantly on the fire-excluded from 500 to 50 stems ha^{-1} ($p = 0.0454$; Fig. 2C). In 2015, the 4x-burned had significantly more oak regeneration (19,253 stems ha^{-1}) than the fire-excluded (13,175 stems ha^{-1}; $p = 0.0454$) or the 3x-burned (11,600 stems ha^{-1}; $p = 0.0101$; Fig. 2B). The burned treatments also had significantly more hard pine stems in 2015 than the fire-excluded (3x: 3,493 and 1,200 vs. 50 stems ha^{-1}; $p = 0.0434$; 4x: $p = 0.0003$; Fig. 2C).

3.2.2. Red maple and other mesophytes

We hypothesized not only that oaks and hard pines would increase significantly during the fire-free interval on burned treatments, but also that oaks would increase relative to red maple and other mesophytic species (H2). We further hypothesized that continued fire-exclusion on the fire-excluded treatment would result in significantly increased densities of red maple and other mesophytic species in the subcanopy and overstory ($\geq$10 cm DBH), as stems in the midstory at the start of the study grew into larger size-classes (H3).

At the start of the study in 1995, overstory and subcanopy red maple density and basal area were similar among treatments, but red maple increased significantly on the fire-excluded throughout the study (Fig. 3A, 3B). In 2007, the fire-excluded treatment had higher overstory red maple stem density (33 stems ha^{-1}) than either fire treatment (3x: 13 stems ha^{-1}, $p = 0.0499$; 4x: 9 stems ha^{-1}, $p = 0.0125$; Fig. 3A), and greater red maple basal area than the 4x-burned (1.44 vs. 0.40 m^2 ha^{-1}, $p = 0.0249$). There was a marginally significant increase in red maple basal area (0 to 0.74 m^2 ha^{-1}, $p = 0.0503$) and stem density (0 to 12.7 stems ha^{-1}; $p = 0.0882$) on the 3x-burned from 1995 to 2007, but not on the 4x-burned (Fig. 3A).

Between 2007 and 2015, overstory red maple continued to increase on the fire-excluded, and in 2015, the fire-excluded had significantly higher red maple density and basal area than the 4x-burned (46 vs. 14 stems ha^{-1}, $p = 0.0069$; 2.14 vs. 0.679 m^2 ha^{-1}, $p = 0.0141$) and marginally significantly higher stem density than the 3x-burned (24 stems ha^{-1}, $p = 0.0660$; Fig. 3A). The relative density of overstory red maple on the fire-excluded also increased significantly between each sampling period (1995–2007: $p = 0.0068$; 2007–2015: $p = 0.0174$; Table 2). This resulted in significantly greater red maple relative density compared to the 4x-burned in 2007 (4x: $p = 0.0361$; 3x: $p = 0.0534$) and compared to both burned treatments in 2015 (4x: $p = 0.0342$; 3x: $p = 0.0131$; Table 2). Overstory red maple density also increased on the 3x-burned treatment from 0 stems ha^{-1} in 1995 to 24 stems ha^{-1} in 2015 ($p = 0.0395$; Fig. 3A), but overstory red maple relative density did not change significantly on either burned treatment throughout the study period (Table 2).

Subcanopy red maple stem density changed significantly on all treatments over the time of this study, increasing on the fire-excluded and decreasing on the burned treatments (Fig. 3B). Red maple stems increased significantly on the fire-excluded from 125 stems ha^{-1} in 1995 to 195 stems ha^{-1} in 2007 ($p = 0.0288$), while fires reduced red maple stems on the 4x-burned from 114 stems ha^{-1} in 1995 to 14 stems ha^{-1} in 2007 ($p = 0.0043$). On the 3x-burned, red maple stem density decreased significantly from 71 stems ha^{-1} in 2007 to 31 stems ha^{-1} in 2015 ($p = 0.0013$), perhaps a delayed response to burning. In 2007, subcanopy red maple density and basal area were significantly different among all treatments (3x and 4x vs. FE: $p < 0.0001$; 3x vs. 4x: $p = 0.0229$). In 2015, the fire-excluded had greater subcanopy red maple stems ($p < 0.0001$) and basal area ($p < 0.0001$; Fig. 3B) than the burned treatments.

Relative density of subcanopy red maple also increased on the fire-excluded, significantly from 37% in 1995 to 66.7% in 2007 ($p = 0.0132$), and was significantly higher than on both burned treatments in 2007 and in 2015 ($p < 0.0001$ for all comparisons; Table 3). In contrast, relative density of red maple in the subcanopy on the 4x-burned decreased marginally from 33% in 1995 to 13% in 2007 ($p = 0.0902$; Table 3). Subcanopy eastern white pine stem density also decreased on the 4x-burned treatment from 50 stems ha^{-1} in 1995 to 10 stems ha^{-1} in 2007 ($p = 0.064$) and to 0 stems ha^{-1} in 2015 (2007–2015, $p = 0.030$; 1995–2015, $p = 0.0067$; Supplement Fig. 1A). This was significantly fewer stems than on the fire-excluded in 2015, which had 23 stems ha^{-1} ($p = 0.0011$), and marginally significantly lower than that on the 3x-burned ($p = 0.0823$; Supplement Fig. 1A). Relative density of subcanopy eastern white pine also decreased on the 4x-burned ($p = 0.0062$), was significantly lower than on the fire-excluded ($p = 0.0151$),

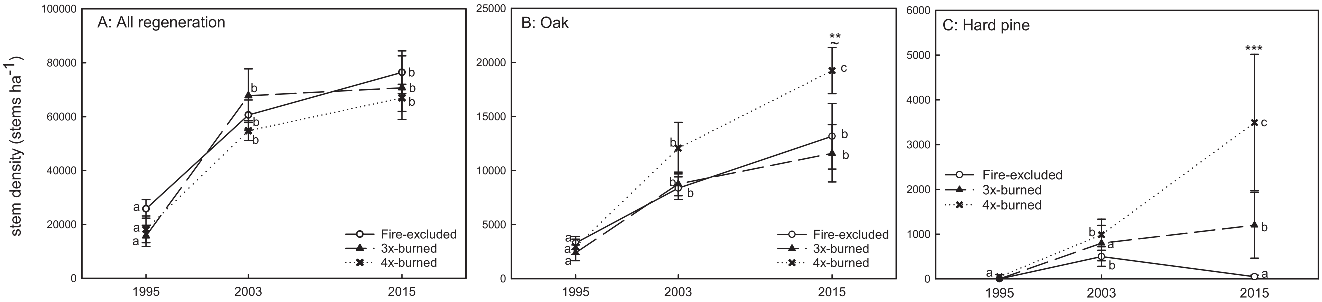

Fig. 2. (A) Total regeneration (<2.0 cm DBH), (B) oak, and (C) hard pine regeneration stem density (stems ha^{-1}) for all treatments before fire (1995), after fire (2007), and after a fire-free interval (2015) on study sites in the Daniel Boone National Forest, Kentucky. Make note of differing y-axis scales. Different lowercase letters indicate significant difference between years within a treatment. If no difference between years, then no letters present. Differences among treatments within year are denoted as follows: *** indicates both burned treatments were significantly different from the fire-excluded, ** indicates only the 4x-burned treatment was significantly different from the fire-excluded, * indicates only the 3x-burned treatment was significantly different from the fire-excluded, ~ indicates that the burned treatments were significantly different from each other (α = 0.05). Error bars are ± 1 standard error of the mean.

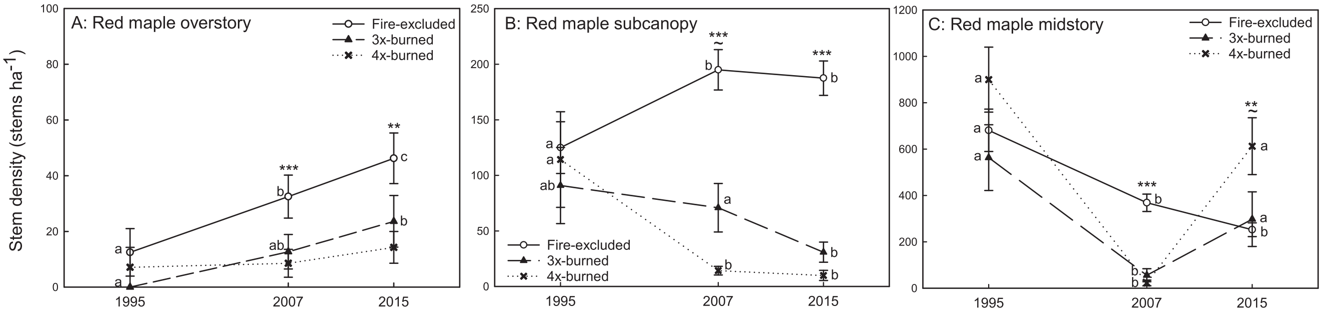

Fig. 3. A) Red maple overstory (≥20 cm DBH), B) red maple subcanopy (10–20 cm DBH), and C) red maple midstory (2–10 cm DBH) stem density (stems ha^{-1}) for size-classes for all treatments before fire (1995), after fire (2007), and after a fire-free interval (2015) on study sites in the Daniel Boone National Forest, Kentucky. Different lowercase letters indicate significant difference between years within a treatment. If no difference between years, then no letters present. Differences among treatments within year are denoted as follows: *** indicates both burned treatments were significantly different from the fire-excluded, ** indicates only the 4x-burned treatment was significantly different from the fire-excluded, * indicates only the 3x-burned treatment was significantly different from the fire-excluded, ~ indicates that the burned treatments were significantly different from each other (α = 0.05). Error bars are ± 1 standard error of the mean.

and marginally significantly lower than on the 3x-burned in 2015 ($p = 0.0972$; Table 3).

Repeated burning also led to decreased midstory stem densities of red maple ($p < 0.0002$; Fig. 3C), eastern white pine ($p < 0.0016$), sourwood ($p < 0.039$), and blackgum ($p < 0.018$) from 1995 to 2007 (Supplement Fig. 1B, 2A, 2B). Midstory red maple also decreased from 1995 to 2007 on the fire-excluded treatment ($p = 0.0047$, Fig. 3C) but not as much as on the burned treatments, and eastern white pine midstory stem density increased significantly on the fire-excluded from 1995 to 2007 (from 219 to 280 stems ha^{-1}, $p = 0.0021$; Supplement Fig. 1B). In 2007, the fire-excluded treatment had significantly greater midstory stem density of red maple ($p < 0.0001$), eastern white pine ($p < 0.0001$), and blackgum ($p < 0.005$) than the burned treatments (Fig. 3C, Supplement Fig. 1B, 2B). Relative stem density of midstory red maple on the fire-excluded was marginally significantly lower than on the 4x-burned in 2007 ($p = 0.0716$), where total stem density was much lower (Table 4). Relative density of midstory eastern white pine was significantly higher on the fire-excluded than on the burned treatments in 2007 ($p = 0.0001$; Table 4). Relative density of midstory sourwood was highest on the 3x-burned in 2007 (FE: $p = 0.0211$; 4x: $p = 0.0104$; Table 4).

During the fire-free interval, stem density of mesophytic species sourwood and red maple increased in the midstory on both burned treatments. On the 3x-burned treatment, midstory red maple stem density ($p = 0.0104$; Fig. 3C) and sourwood ($p < 0.0001$; Supplement Fig. 2A) increased; on the 4x-burned treatment, red maple ($p = 0.0128$), eastern white pine ($p = 0.0353$; Supplement Fig. 1B), sourwood ($p < 0.0001$) and blackgum ($p < 0.0001$; Supplement Fig. 2B) increased. The only significant change in the midstory on the fire-excluded from 2007 to 2015 was decreased midstory blackgum stem density ($p = 0.0368$). In 2015, the 4x-burned had significantly more midstory red maple (3x: $p = 0.0247$; FE: $p = 0.0053$) and sourwood stem density ($p < 0.0001$ for both) than the 3x-burned or the fire-excluded, as well as much higher total midstory stem density (3x: $p < 0.0001$; FE: $p = 0.0015$; Table 1). However, relative density of midstory red maple was marginally significantly lower on the 4x-burned compared to the 3x-burned ($p = 0.055$; Table 4), while relative density of midstory red maple was marginally significantly higher on the 3x-burned compared to the fire-excluded ($p = 0.077$; Table 4). Eastern white pine midstory absolute and relative density remained significantly higher on the fire-excluded in 2015 than on the burned treatments ($p < 0.0001$ for all comparisons; Supplement Fig. 1B, Table 4). Sourwood relative density in 2015, on the other hand, was significantly higher on the burned treatments than on the fire-excluded ($p < 0.0001$ for all comparisons; Table 4).

Despite the increases in stem density of mesophytic species on the 4x-burned, it is notable that midstory oak stem density was also significantly greater on the 4x-burned ($p < 0.0001$; Fig. 1C), as was the relative density of oak midstory stems compared to the fire-excluded in 2015 ($p = 0.0072$, Table 4). On the 3x-burned, the decline in relative density of midstory oaks during the fire-free interval corresponded to a marginally significant increase in relative density of midstory red maple ($p = 0.0815$) and a significant increase in relative density of midstory sourwood ($p = 0.0004$; Table 4).

Among the mesophytic species, red maple regeneration increased on all treatments from 1995 to 2003 (FE: $p < 0.0001$, 3x: $p = 0.0030$, 4x: $p = 0.0011$; Fig. 4A), and eastern white pine increased significantly on the fire-excluded ($p = 0.0125$) and marginally significantly on the 3x-burned ($p = 0.0900$; Fig. 4B). In 2015, the fire-excluded had significantly more red maple regeneration than the 4x-burned (46,975 vs. 28,933 stems ha^{-1}; $p = 0.0244$; Fig. 4A); red maple on 3x-burned was similar to the other two treatments (39,108 stems ha^{-1}; FE: $p = 0.466$, 4x: $p = 0.168$). From 2003 to 2015, red maple regeneration increased on the fire-excluded (30,300 to 46,975 stems ha^{-1}; $p = 0.0036$) and the 3x-burned (26,523 to 39,108 stems ha^{-1}; $p = 0.0014$). Also during this period, eastern white pine regeneration increased on the 4x-burned (800 to 2000 stems ha^{-1}; $p = 0.0014$) and on the 3x-burned (215 to 1077 stems ha^{-1}; $p = 0.0085$; Fig. 4B).

4. Discussion

After a 10-year fire-free interval we found lower total basal area on the burned treatments compared to the fire-excluded treatment, as hypothesized (H1). However, we did not anticipate finding the greatest reductions in basal area on the 4x-burned, or the continued mortality of overstory and subcanopy stems. We also did not expect that the decrease in basal area in these larger size-classes would trigger the very large increase in midstory stems on the 4x-burned or, more generally, that the 3x- and 4x-burned treatments would respond so differently during the fire-free period. It is likely that the increased light from reduced overstory and subcanopy created the conditions for increased ingrowth of stems into the midstory as was seen on the 4x-burned.

The decrease in basal area and stem density on the 4x-burned treatment suggests that repeated prescribed fire can lead to delayed fire mortality of overstory stems, as has been found elsewhere (Keyser et al., 2017). Throughout the study site we found patchy mortality of overstory stems that had occurred since the last prescribed fire, and which appeared to be the result of wind or ice storms and most prevalent on the burned treatments (personal observations), where fire may have served as a predisposing disturbance agent. Repeated prescribed fire may set the stage for enhanced overstory mortality by weakening trees (Hutchinson, 2012a). Such disturbance impacts could be expected to be variable across the landscape, and it is possible that a fourth burn created greater potential for delayed mortality of overstory and subcanopy trees on the 4x-burned compared to the 3x-burned.

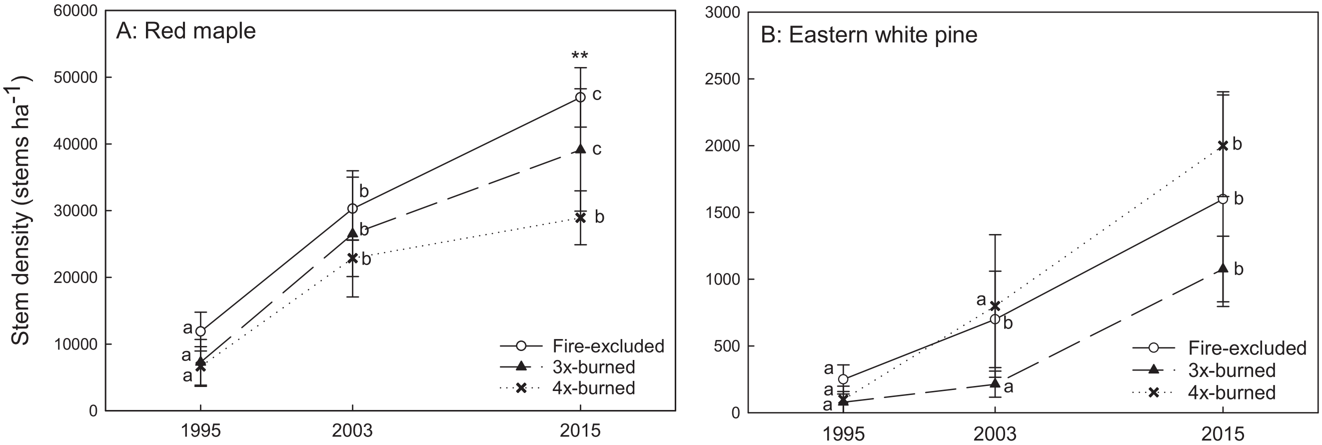

Fig. 4. A) Red maple and B) eastern white pine regeneration (<2.0 cm DBH) stem density (stems ha^{-1}) for all treatments before fire (1995), after fire (2007), and after a fire-free interval (2015) on study sites in the Daniel Boone National Forest, Kentucky. Make note of differing y-axis scales. Different lowercase letters indicate significant difference between years within a treatment. If no difference between years, then no letters present. Differences among treatments within year are denoted as follows: *** indicates both burned treatments were significantly different from the fire-excluded, ** indicates only the 4x-burned treatment was significantly different from the fire-excluded, * indicates only the 3x-burned treatment was significantly different from the fire-excluded, ~ indicates that the burned treatments were significantly different from each other ($\alpha = 0.05$). Error bars are ± 1 standard error of the mean.

Supporting H2, we found increased oak stem density in the midstory and the regeneration size-classes on the 4x-burned, which had the lowest total basal area in 2015. Relative density of midstory oaks also increased, signaling a shift to oaks relative to red maple and other mesophytes. While the 3x-burned had lower total stem density and basal area than the fire-excluded, overstory stem density and basal area were not significantly different from that of the fire-excluded, and overstory stem density was significantly greater than the 4x-burned. Likely as a result of these nominal changes in stand structure on the 3x-burned, oak stem density in the midstory and regeneration size-classes did not increase in this treatment during the fire-free interval. Thus, our hypothesis that midstory and regeneration size-class oaks would increase on burned treatments was only supported on the 4x-burned.

We also found the only records of midstory hard pine stems on the 4x-burned, and hard pine regeneration increased on the burned treatments while it decreased on the fire-excluded. Recent research on shortleaf pine demonstrated that regeneration of this species in oak-pine forest types increases with increasing shortleaf pine in the overstory and increasing canopy openness (Ojha et al., 2019). Our experimental design did not lend itself to assessing these relationships directly, but it is notable that shortleaf and the other hard pines (pitch pine and Virginia pine) were measured in the midstory only on the 4x-burned treatments. Similarly, in a study of the vegetation response to a single wildfire in a site within the Red River Gorge Geological Area very similar to this study, we found decreasing canopy openness and increasing hard pine regeneration with increasing composite burn index (CBI; Black et al., 2018).

Unfortunately, in the context of managing to maintain and enhance oak dominance in this forest ecosystem, some of the increase in midstory stem density on the burned treatments, especially the 4x-burned, likely occurred because of a large decline in overstory and subcanopy basal area, some of which was due to oak mortality. Mortality of stems following prescribed fire is generally expected to be lower for oaks than for mesophytic species (Keyser et al., 2018). However, there is new evidence that delayed mortality can occur among older oaks (Robbins et al., 2022), especially when there has been a long fire-free period prior to burning, during which time the depth of the soil organic layer has increased (Carpenter et al., 2020). In addition to higher light levels from lower basal area, the significant increase in midstory oaks on the 4x-burned may have been the result of basal sprouting from killed overstory oaks.

Other studies that examined oak recruitment following a fire-free period did not see dramatic increases in oak midstory stem densities, but the fire-free interval did not extend beyond 7 years (Hutchinson et al., 2012b; Keyser et al., 2017). Keyser et al. (2017) noted that a fire-free period following prescribed fire may be a more important factor than the number of fires in determining the regeneration response. In that study, there was a stronger oak sapling response in sites with fewer fires and a longer fire-free interval (2 fires over seven years vs. 5 fires over nine years). A fire-free interval enhanced oak seedling growth and recruitment in this study as well, but we found a stronger oak response in the 4x-burned compared to the 3x-burned, suggesting the need for a more open subcanopy and overstory than what was attained through repeated prescribed burning after decades of fire suppression. Others have noted that greater reduction in basal area (via natural disturbance or mechanical manipulation) may be necessary to facilitate a significant increase in oak regeneration than can readily be achieved by fire alone (Brose et al., 2014), and this study supports that idea.

Despite the positive findings of increased oaks in the midstory and regeneration size-classes after a fire-free interval on the 4x-burned, we found significant increases in stem density of mesophytes in both burned treatments in these size-classes. Notably, despite increased absolute red maple stem density, relative density of midstory red maple decreased on the 4x-burned and relative density of oaks increased. In a study of the vegetation response to a single wildfire in a nearby site, we found that red maple was largely agnostic to fire severity, responding similarly across plots with widely varying CBI (Black et al., 2018). Despite this even response of red maple regeneration to CBI (which varied from 0.2 to 2.5 on a scale of 0–3; Key and Benson, 2006), oaks and pines responded with greater regeneration and growth into the midstory in sites with higher CBI and greater canopy openness.

We found very strong evidence for a legacy effect of long-term fire suppression. Red maple stems remaining on the site after repeated fire were still viable and grew with vigor into the canopy gaps. While there were many more oak stems on the 4x-burned than on the other two treatments, and more oaks (and hard pines) than before burning, maples still dominated the species composition. This finding suggests a caveat to the suggestion that fire-free intervals extend for 10–30 years to support oaks (Arthur et al., 2012; Dey and Schweitzer, 2015; Knapp et al., 2017). In forests where red maple and eastern white pine are highly competitive mesophytes that regenerate and thrive in dense midstories (Blankenship and Arthur, 1999b; Blankenship and Arthur, 2006; Hutchinson et al., 2005), a fire-free period longer than 10 years may allow for too much dominance by maples. High densities of red maple and eastern white pine regeneration despite repeated burning instead signal the need for additional management.

Importantly, this study also showed that continued exclusion of fire on the fire-excluded treatment led to a steady increase in red maple stems and the relative density of red maple in the overstory and subcanopy, with red maple essentially switching places with oaks in subcanopy dominance (H3). Simultaneous with these changes, the relative density of oaks in the fire-excluded treatment decreased in the subcanopy (though not significantly). The rapid ingrowth of maples into these larger size-classes with continued fire exclusion is emblematic of the ongoing mesophication and densification process unfolding across many upland forest ecosystems in this region (Hanberry et al., 2020b; Nowacki and Abrams, 2008). This dramatic influx of a mesophytic species into the canopy signals the long-term changes in the species composition of these forests that will continue to set the stage for future management potential.

5. Management implications

Our study highlights four key findings that are highly relevant to managers of upland oak and oak-pine forests in the Central Appalachian forest regions. First, where fire has been suppressed for many decades, repeated prescribed fire can set the stage for improvements in regeneration and growth of oaks and other pyrophytes by reducing stem density and basal area and suppressing mesophytic species, such as red maple and eastern white pine. Second, in burned sites, a fire-free period allows for the growth and development of oak seedlings into the midstory, where they can reach a size that is more resistant to top-kill or mortality. Third, while these conditions are necessary for enhancing oak growth into the midstory, they are not sufficient, for two reasons. (1) Repeated fire alone does not open the canopy sufficiently for enhanced oak regeneration and growth (Arthur et al., 2015; Blankenship and Arthur, 2006; Hutchinson et al. 2012a), but requires additional mortality of overstory trees, which can occur through natural disturbances and further management. (2) The legacy of fire suppression over many decades prior to contemporary management with prescribed fire leads to increased stem density of mesophytic species, and these species (especially red maple) are suppressed but not killed by repeated top-kill and are still competitive across conditions of light availability. Finally, this study demonstrates clearly that continuation of long-term fire suppression leads to ongoing mesophication and increased dominance of the overstory by mesophytic species. In upland forest landscapes that developed in the absence of fire for many decades, maintenance of oak- and pine- dominated forests will require ongoing management. Such management includes creating more open canopies using prescribed fire or other disturbances, followed by periods without fire, coupled with ongoing management of mesophytic species to address the legacy effects of prior fire suppression and ongoing mesophication.

Authors' contributions

MA designed and implemented the original study. ZP led the field crew in data collection in 2015. BA and ZP conducted the data analysis. BA, ZP and MA contributed to writing the manuscript. MA acquired funding and supervised study implementation, methodology, data analysis, and writing. All authors contributed to revisions and approved the final draft.

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.

Data availability

Data will be made available on request.

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Availability of Data and Materials

The datasets generated or analyzed during this study are not publicly available due to concerns regarding study plot locations in close proximity to a heavily used public recreation area, but are available from the corresponding author on reasonable request.

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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.2023.121367.

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