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Repeated burning alters the structure and composition of hardwood regeneration in oak-dominated forests of eastern Kentucky, USA

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ABSTRACT

The exclusion of anthropogenic fire is a primary factor responsible for the 'mesophication' of eastern oak (*Quercus*) forests and resultant oak regeneration problems. Consequently, the reintroduction of fire is increasingly used to promote the establishment and growth of oak and hickory (*Carya*) and control competition from shade-tolerant species (e.g., red maple (*Acer rubrum*)) in the forest understory. In this study, we examined the effects of fire frequency on the abundance of prominent species in the woody regeneration layer in oak-dominated forests of eastern Kentucky. Treatments included: (1) fire-excluded (FE); (2) frequent fire (FF) – five burns over nine years, and (3) less-frequent fire (LFF) – two burns over seven years. Prior to burning (2002) and again five and seven growing seasons following the cessation of burning in the FF and LFF treatments (2015), respectively, we inventoried tree species in the woody regeneration layer into three size classes: (1) small seedlings (stems < 0.6 m), (2) large seedlings (≥0.6 m and <1.2 m) and (3) small saplings (≥1.2 m and <3.8 cm diameter at breast height). Pre- and postburn, the regeneration layer was dominated by non-Oak-Hickory species, and although Oak-Hickory regeneration was abundant the majority of stems were <0.6 m. For Oak-Hickory, significant treatment effects were limited to the large seedling and small sapling size classes. For large Oak-Hickory seedlings, density was significantly greater in the LFF than FE treatment. For small Oak-Hickory saplings, density in the LFF treatment was ~17 and ~4 times greater than in the FE and FF treatments, respectively. This study provides support for the notion that fire-free periods may be more of a factor controlling the abundance and composition of the woody regeneration layer than simply the number of burns. However, despite greater stem density, the fate of the Oak-Hickory regeneration layer that developed in response to the LFF treatment is uncertain, as the density of non-oak competitors remains high. Additional treatments (e.g., targeted herbicide application, additional burning) may be necessary to reduce the abundance of non-oak species and increase the likelihood of continued recruitment Oak-Hickory should natural or silvicultural release events occur.

1. Introduction

In the eastern United States, oak (*Quercus*) species have been a dominant component of the forests for millennia (Delcourt and Delcourt, 1997, 1998). Today, Oak-Hickory (*Carya*) is the most dominant forest type in the eastern United States, comprising 34% (57.4 million ha) of the forested landbase (Oswalt et al., 2014). Changes in disturbance regimes precipitated by Euro-American settlement coupled with factors that include climate variability, extirpation of species, and changes in land-use interact to influence structure, composition, and regeneration potential of eastern Oak-Hickory (*Quercus-Carya*) forests (Gragson and Bolstad, 2006; McEwan et al., 2011). In Appalachian hardwood forests, a relatively low disturbance frequency over the last century (Hart and Grissino-Mayer, 2008; Hart et al., 2012) has facilitated the development of dense understories (i.e., sapling and midstory) and hastened the succession of these forests towards shade-tolerant species such as red maple (*Acer rubrum*), sugar maple (*A. saccharum*), blackgum (*Nyssa sylvatica*), and American beech (*Fagus grandifolia*) (Hart and Grissino-Mayer, 2008). The ecological and economic ramifications associated with the gradual replacement of oak forests to those dominated by non-oak species (Fei et al., 2011) are wide-ranging and include decreased water yield (Caldwell et al., 2016) and direct and indirect effects on population dynamics of game and non-game wildlife species (McShea et al., 2007).

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Although a multitude of interacting forces control stand dynamics and successional patterns (McEwan et al., 2011), fire, or more accurately, lack thereof, is often identified as the primary factor responsible for the 'mesophication' of eastern oak forests and associated oak regeneration and recruitment problems (Abrams, 1992; Nowacki and Abrams, 2008). Dendroecology (Shumway et al., 2001; McEwan et al., 2007), paleoecology (Delcourt et al., 1998; Fesenmyer and Christensen, 2010), and witness tree (Thomas-Van Gundy and Nowacki, 2013) studies provide evidence that periodic fire (mean fire return interval of 7.7 years (range 1–29 years); Lafon et al., 2017) was a factor contributing to the development and maintenance of Oak-Hickory forests across varying spatial and temporal scales, with the increase in the abundance of shade-tolerant species and onset of oak regeneration problems correlated with fire exclusion and suppression efforts in the early to mid-1900s (Shumway et al., 2001; Lafon et al., 2017). As such, reintroduction of fire, with frequency, intensity, and seasonality of burns informed by historic fire regimes (e.g., Guyette et al., 2006; Flatley et al., 2013; Aldrich et al., 2014), is actively integrated into forest management plans on public and private lands.

Successful oak regeneration and recruitment following disturbance is dependent upon the existence of a large number of competitive (i.e., large) oak seedlings in the forest understory prior to disturbance (Sander, 1972; Loftis, 1990a). In Appalachian hardwood forests, oak seedlings, which are only moderately tolerant of shade, are unable to develop into larger and more competitive size classes under dense shaded understories (Crow, 1992; Loftis, 1990b; Lorimer et al., 1994). Thus, small seedlings, which dominate the forest understory, are unable to compete with shade-tolerant species already present in the woody regeneration layer or new seedlings of species such as yellow-poplar (*Liriodendron tulipifera*) and sweet birch (*Betula lenta*) that establish following canopy-reducing disturbance(s) (Loftis, 1983; Miller et al., 2006). There are numerous critical processes associated with the oak regeneration process – flowering and acorn production, germination and seedling establishment, seedling development, and overstory recruitment – where disturbance, including prescribed fire, may alter the probability of successful regeneration (Arthur et al., 2012). Fire may be of particular importance to the development of larger competitive oak and hickory seedlings by controlling stem density and resultant light availability and reducing competition from non-oak species in the woody regeneration layer (Van Lear and Waldrop, 1989; Brose, 2014).

Short-term results (e.g., <3 growing seasons post-fire) from prescribed fire studies in eastern mixed-oak forests suggested repeated burning at regular intervals does little to enhance oak and hickory seedling development or control competition from shade-tolerant species in the woody regeneration layer (Hutchinson et al., 2005; Blankenship and Arthur, 2006; Alexander et al., 2008). Mechanisms underlying fire's limited impact include only minor effects on stand structure and resultant understory light availability and rapid and prolific sprouting of top-killed non-oak individuals (Arthur et al., 1998; Chiang et al., 2005; Iverson et al., 2008). Since publication of these early studies, understanding of the intricacies of the role of fire in establishing and maintaining present-day oak forests has advanced. For example, retrospective (Dey and Guyette, 2000; Signell et al., 2005; McEwan et al., 2007) and manipulative field studies (Peterson and Reich, 2001; Hutchinson et al., 2012b; Knapp et al., 2015) from oak-dominated systems suggest spatial variability in fire occurrence and temporal variability in fire frequency and corresponding fire-free periods and fire severity act as ecological filters selecting species with regeneration traits adapted to local and regional fire regimes (Pausas et al., 2004; Myers and Harms, 2011; Hollingsworth et al., 2013). In upland Oak-Hickory forests regeneration traits favored by fire are typified by oak and hickory species, and include high root to shoot ratios (Kolb et al., 1990), hypogeal germination, and superior sprouting and growth following top-kill (Brose et al., 2013).

Forests of the Cumberland Plateau are comprised of a diverse suite of species that represent a variety of life history and functional traits. Although species composition varies with topography and associated gradients in moisture availability, upland Oak-Hickory forest types dominate the landscape (McNab, 2011). Similar to other eastern oak forests, land-use history and a decrease in the frequency of exogenous disturbance events has, in part, created forest conditions less favorable to regeneration and recruitment of oak and hickory species, particularly on more productive mesic sites where securing oak regeneration is particularly problematic (Loftis, 1990a; Schweitzer and Dey, 2011). Consequently, the reintroduction of fire is increasingly viewed as a tool managers can use to promote the establishment and development of fire-adapted tree species, including oak and hickory, in the forest understory and to facilitate eventual recruitment into the forest canopy (Brose, 2014). The primary objective of this study was to examine the effects of alternative prescribed fire regimes characterized by frequent fire versus less frequent fire on the abundance of prominent species groups in the regeneration layer across a topographically complex landscape characterized by a productivity or moisture availability gradient. Given the longer-term nature of this study, we hypothesized: (H1) Oak and hickory in the woody regeneration layer will increase in abundance in response to fire, with the greatest increase occurring as a result of more frequent fire; (H2) Fire will reduce the abundance of shade-tolerant species in the woody regeneration layer, with the greatest reduction occurring as a result of more frequent fire; and (H3) the effects of fire, regardless of fire frequency, will vary across the landscape, with the greatest effects on the density and size distribution of woody regeneration occurring on more xeric, less productive portions of the landscape.

2. Materials and methods

2.1. Study site

This study was conducted on the Cumberland Ranger District of the Daniel Boone National Forest located in the Cumberland Plateau Physiographic Province in eastern Kentucky (38.1°N, 83.5°W). January and July mean daily temperature (30-year normal, 1981–2010) is 2 °C and 24.6 °C, respectively (http://www.ncdc.noaa.gov.). Mean annual precipitation is approximately ~1250 mm (http://www.ncdc.noaa.gov). Topography is varied, with elevations between 260 m and 360 m and slopes ranging from 0% to 75%. Soils throughout the study area are classified as Typic Hapludults, Typic Hapludalfs, Ultic Hapludalfs, and Typic Dystrochrepts (Avers, 1974). On ridges and steep slopes, soils are typically loamy to clayey, possess low soil moisture holding capacity, and are low in fertility, while soils on lower slopes, coves, and terraces are characterized by higher organic matter and greater soil moisture holding capacity (Jones, 2005).

Forests within the study area are second-growth forests that range in age from 80 to 110 years. These forests originated from heavy cutting in the early 20th century and have experienced fire exclusion/suppression and minimal disturbance over the 80+ years of stand development. White oak (*Quercus alba*) site index (base-age 50) varied with topographic position and aspect, and ranged from 15 m to 34 m. Prior to treatment, basal area (BA) and stem density of the overstory layer (stems $\geq$ 20 cm diameter at 1.37 m above groundline (dbh)) averaged 21.7 m^2 ha^{-1} and 211 stems ha^{-1}, respectively, and BA and stem density of the midstory layer (stems 10–20 cm dbh) averaged 4.0 m^2 ha^{-1} and 249 stems ha^{-1}, respectively (Arthur et al., 2015). Across the study area, oak and hickory species combined represented 34% and 80% of the pretreatment midstory and overstory BA, respectively (Arthur et al., 2015). The sapling layer (stems 2–10 cm dbh) was comprised of shade-tolerant species, including red maple, sugar maple (*Acer saccharum*), serviceberry (*Amelanchier arborea*), blackgum (*Nyssa sylvatica*), and sourwood (*Oxydendrum arboreum*).

2.2. Experimental design and data collection

Three blocks (Wolf Pen, Chestnut Cliffs, and Buck Creek), each between 200 and 300 ha, were located on the Cumberland Ranger District. Each block was divided into three stands, each between 58 and 116 ha. One of three treatments was randomly assigned to each of the three experimental units in each block. Treatments were: Fire-Excluded (FE), Frequent Fire (FF), and Less Frequent Fire (LFF). Between 8 and 12 measurement plots were established within each of the nine stands. During the course of this study, 5 of the 10 FE plots in the Wolf Pen block and 1 of the 11 FE plots in the Buck Creek block were accidentally burned during unplanned fire and were, therefore, removed from analyses. Plots were 10 m $\times$ 40 m (0.04 ha), with the long axis oriented parallel to the contour. Species composition of stems $\geq$ 2 cm dbh recorded prior to treatment (Arthur et al., 2015) was used to categorize plots into one of three moisture classes: Subxeric, Intermediate, or Submesic (McNab et al., 2007; McNab and Loftis, 2013).

At the center of each plot, a 0.004 ha circular subplot was established in which tree regeneration was inventoried by species (up to a maximum of 25 individuals per species$*$size class combination in a given 0.004 ha regeneration subplot) in the following size classes: (1) small seedlings (stems < 0.6 m in height); (2) large seedlings (stems $\geq$ 0.6 m in height but <1.2 m in height); and (3) small saplings (stems $\geq$ 1.2 m in height but <3.8 cm dbh). These size classes were chosen to reflect the positive relationship between oak and hickory regeneration potential and seedling/sapling size (Loftis, 1990a) and to maintain consistency among other prescribed burning and silvicultural studies being conducted in the region (e.g., Schweitzer and Dey, 2015). Top-killed stems with multiple basal sprouts were recorded as one individual. Sampling of the tree regeneration pool (stems < 3.8 cm dbh) occurred in 2002 (pretreatment) and 2015.

Prescribed burns were implemented by the USDA Forest Service. All fires were conducted between March 24th and April 18th. For the FF treatment, five prescribed burns were conducted over a nine year period, occurring in 2003, 2004, 2006, 2008, and 2011. For the LFF treatment, two burns were conducted over a seven year period in 2003 and 2009. No manipulation of vegetation occurred in the FE treatment. In 2003, prescribed burns in two of the three blocks were aerially ignited. All other burns were ignited via drop torches. Specific information regarding burn logistics (e.g., ignition patterns, weather, and fuel moisture conditions), fire temperatures, and direct fire effects for all but the most recent burn conducted in 2011 are detailed by Arthur et al. (2015).

We did not monitor the establishment of new individuals via seed or root suckering, nor did we monitor an individual seedling's survival and growth. This is an important limitation, as the changes in the size distribution and composition of the woody regeneration layer reported here could be masked by species-specific patterns of seedling establishment, survival, and growth along with basal sprouting of top-killed stems (Wang et al., 2005; Alexander et al., 2008; Royse et al., 2010). Because of this, our results reflect a point-in-time description of the effects of treatment and moisture class on the woody regeneration layer.

2.3. Data analysis

We used a linear mixed-effects model under a split-plot repeated measures design to analyze absolute density (stems ha^{-1}) of small and large seedlings and small saplings in 2002 and 2015 for each of the five species groups identified in Table 1 (Maples, Oak-Hickory, Other, Sassafras, and Tolerant). Similarly, we analyzed relative density of species groups within the small sapling layer. For each analysis, treatment (FE, FF, LFF) was the whole-plot factor, moisture class (Subxeric, Intermediate, Submesic) was the split-plot factor, and year was the repeated factor. Treatment, moisture class, and year along with all possible interactions were fixed effects and block and block$*$treatment were random effects. The covariance structure used to account for repeated measurements was compound symmetry or heterogeneous compound symmetry. Analyses were conducted using the MIXED procedure in SAS v. 9.4 (SAS Institute, 2011). The GROUP option was utilized to specify heterogeneity in the residual covariance (grouping factors included moisture class, treatment, treatment$*$year, or moisture class$*$year depending on the species group-size class combination analyzed) (Littell et al., 2006). Significant interactions were examined using the SLICE option. Following significant *F*-tests, or partitioned *F*-tests in the case of interactions, differences among least-square means were detected using Fishers Least Significant Difference. When necessary, data were square-root transformed to achieve normality and homoscedasticity. Analyses were significant at alpha = 0.05.

3. Results

3.1. General characteristics of the woody regeneration layer

Across treatments, moisture classes, and species groups, the density of the woody regeneration layer averaged 22,558 and 30,096 stems ha^{-1} in 2002 and 2015, respectively. Before and after treatments, woody regeneration was dominated by shade-tolerant species, with the Maple and Tolerant species groups comprising an average of 43% of the woody regeneration layer over the course of the study. In comparison, species in the Oak-Hickory group constituted only 22% and 28% of the woody regeneration layer in 2002 and 2015, respectively. Small seedlings (<0.6 m tall) dominated the regeneration layer in each species group, representing 92% of the regeneration layer in 2002 and 75% of the woody regeneration layer in 2015 (Fig. 1). The Sassafras group experienced the greatest proportional increase in the combined large seedling and small sapling size classes, increasing from 11% in 2002 to 44% in 2015. In contrast, the Maple group experienced the lowest proportional increase in the combined large seedling and small sapling layers, increasing from 6% to 10% between 2002 and 2015.

3.2. Small seedlings

Fire, regardless of frequency or moisture class, had no effect on the density of small seedlings for any of the five species groups (Table 2). Across treatments and moisture classes, small seedling density of Oak-Hickory in 2015 was greater by 2354 seedlings ha^{-1} than in 2002 while small seedling density of Sassafras in 2015 was lower by 1090 seedlings ha^{-1} than in 2002 (Table 3). Absolute density of small seedlings for the Oak-Hickory, Other, and Sassafras species groups varied across moisture classes (Table 2). Across years and treatments, absolute density of small seedlings for the Oak-Hickory and Sassafras groups was significantly greater on the Subxeric and Intermediate versus Submesic portions of the landscape. For the Other species group, absolute small seedling density increased as moisture availability increased (Table 3). Small Maple seedling density was 1417 ha^{-1} greater on

Table 1
Species comprising the Oak-Hickory, Maple, Sassafras, Other, and Tolerant species groups.

Oak-Hickory	Sassafras	Maple	Other	Tolerant
White oak (*Quercus alba*)	Sassafras (*Sassafras albidum*)	Red maple (*Acer rubrum*)	White ash (*Fraxinus americana*)	Serviceberry (*Amalanchier arborea*)
Scarlet oak (*Quercus coccinea*)		Sugar maple (*Acer saccharum*)	Cucumbertree (*Magnolia accuminata*)	Buckeye (*Aesculus flava*)
Chestnut oak (*Quercus montana*)			American chestnut (*Castenea dentata*)	Musclewood (*Carpinus caroliniana*)
Northern red oak (*Quercus rubra*)			Eastern white pine (*Pinus strobus*)	Flowering dogwood (*Cornus florida*)
Black oak (*Quercus velutina*)			Sweet birch (*Betula lenta*)	Elm species (*Ulmus*)
Hickory species (*Carya*)			Black walnut (*Juglans nigra*)	American beech (*Fagus grandifolia*)
			Yellow-poplar (*Liriodendron tulipifera*)	Hackberry (*Celtis occidentalis*)
			Black locust (*Robinia pseudoacacia*)	Holly species (*Ilex*)
			Black cherry (*Prunus serotina*)	Mulberry (*Morus rubra*)
			Shortleaf pine (*Pinus echinata*)	Blackgum (*Nyssa sylvatica*)
			Virginia pine (*Pinus virginiana*)	Ironwood (*Ostrya virginiana*)
			Umbrella magnolia (*Magnolia tripetala*)	Sourwood (*Oxydendrum arboreum*)
			Blue ash (*Fraxinus quadrangulata*)	Pawpaw (*Asimina triloba*)
			Bigtooth aspen (*Populus grandidentata*)	Persimmon (*Diospyros virginiana*)
				Eastern redbud (*Cercis canadensis*)
				Alerternate-leaf dogwood (*Cornus alternifolia*)

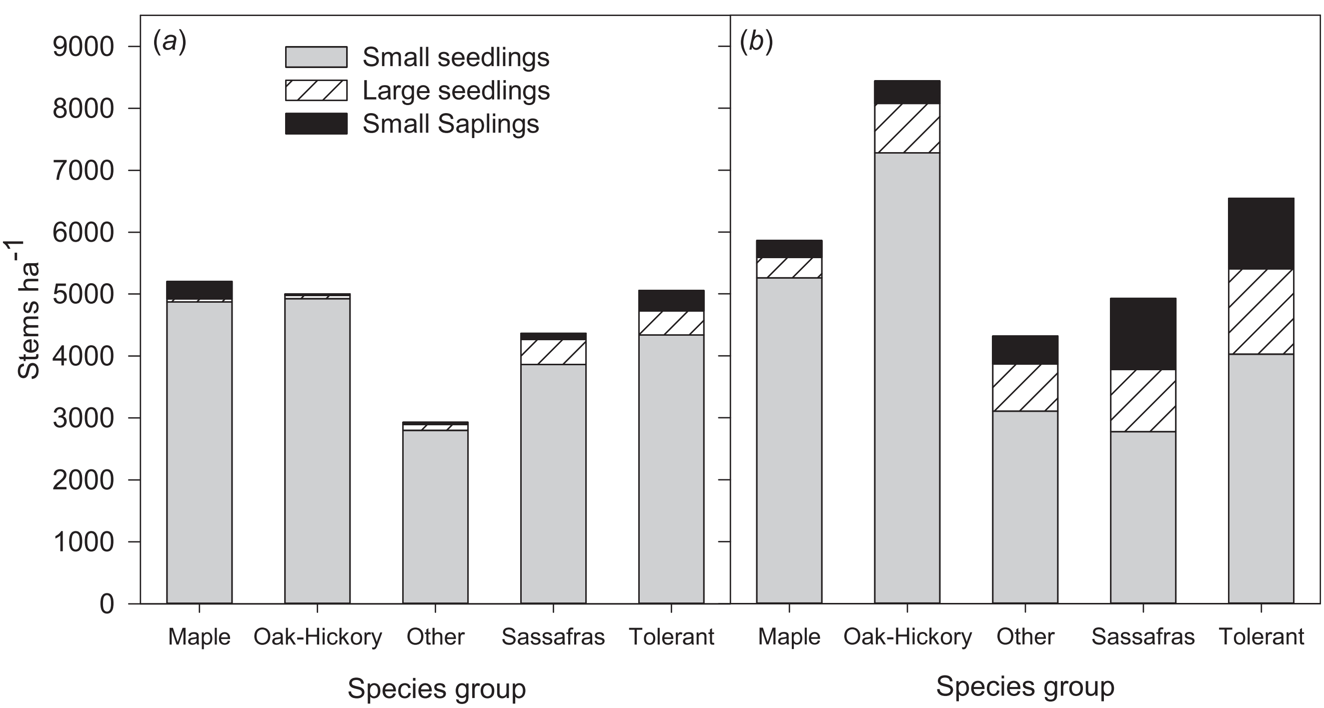

Fig. 1. Woody regeneration by size class and species group in 2002 (pretreatment) and 2015 within the Daniel Boone National Forest, Kentucky.

Subxeric sites in 2015 than in 2002, but did not vary significantly among the moisture classes in either year.

3.3. Large seedlings

Fire significantly affected the absolute density of large Oak-Hickory seedlings (stems $\geq$ 0.6 m and <1.2 m tall), and this effect varied by year (Table 2). In 2002, prior to treatment, large Oak-Hickory seedling density averaged only 49 stems ha^{-1} across the FE, FF, and LFF treatments. Large Oak-Hickory seedling density increased between 2002 and 2015 in both the FF and LFF treatments (Fig. 2a). However, by 2015, large Oak-Hickory seedling density was significantly greater only in the LFF treatment compared to the FE treatment, with large Oak-Hickory seedlings averaging 189, 752, and 1310 ha^{-1} in the FE, FF, and LFF treatments, respectively. Regardless of frequency, fire had no significant impact on the density of large seedlings in the Maple, Other, Sassafras, and Tolerant species group, However, significantly greater large seedling density in 2015 than in 2002 for these four competitor species groups provides evidence of recruitment into this size class regardless of treatment or moisture class (Fig. 3). Large Oak-Hickory seedling density varied across moisture classes, but only in 2015. In 2002, large Oak-Hickory seedling density averaged 55 ha^{-1} on Subxeric, Intermediate, and Submesic sites (Fig. 2b). By 2015, large

Table 2
P-values associated with the split-plot analysis of absolute density (stems ha^{-1}) of small seedlings, (stems < 0.6 m tall), large seedlings (stems $\geq$ 0.6 m tall and <1.2 m tall), and small saplings (stems $\geq$ 1.2 m tall and <3.8 cm dbh) as well as relative density of small saplings by species group in the Danielle Boone National Forest, Kentucky. TRT = treatment (FE, FF, LFF), MC = moisture class (Subxeric, Intermediate, Submesic), YR = year (2002, 2015). Bold values indicate significance at alpha = 0.05.

Fixed effect	df	Maple	Oak-Hickory	Other	Sassafras	Tolerant
		Small seedling density (stems ha^{-1})				
TRT	2	0.9747	0.7112	0.1945	0.3847	0.1503
MC	2	0.8183	**0.0005**	**0.0011**	**0.0056**	0.5291
TRT*MC	4	0.7765	0.4372	0.3381	0.0827	0.4811
YR	1	0.0924	**<0.0001**	0.4359	**0.0133**	0.3802
TRT*YR	2	0.0743	0.4363	0.8312	0.8179	0.7206
MC*YR	2	**0.0328**	0.6274	0.1928	0.2557	0.2125
TRT*MC*YR	4	0.7067	0.6421	0.7471	0.5154	0.1489
		Large seedling density (stems ha^{-1})				
TRT	2	0.4353	0.0872	0.5481	0.5490	0.7205
MC	2	0.1513	**0.0008**	**0.0398**	0.3094	0.1262
TRT*MC	4	0.9967	0.7718	0.6942	0.9889	0.9284
YR	1	**<0.0001**	**<0.0001**	**<0.0001**	**0.0198**	**<0.0001**
TRT*YR	2	0.5961	**0.0438**	0.5378	0.2460	0.2586
MC*YR	2	0.0946	**0.0461**	0.3148	0.1805	0.7862
TRT*MC*YR	4	0.7624	0.7090	0.2127	0.8017	0.8181
		Small sapling density (stems ha^{-1})				
TRT	2	0.8246	**0.0383**	0.5516	**0.0100**	0.9270
MC	2	0.7084	**0.0428**	0.0673	0.5304	0.1947
TRT*MC	4	0.6996	0.4292	0.9553	0.5918	0.9394
YR	1	0.8487	**<0.0001**	**0.0019**	**<0.0001**	**0.0007**
TRT*YR	2	0.9208	**0.0104**	0.4538	**0.0117**	0.8949
MC*YR	2	0.3787	**0.0236**	0.2623	0.0603	0.1185
TRT*MC*YR	4	0.8164	0.3957	0.9199	0.1712	0.2403
		Small sapling relative density (%)				
TRT	2	0.6829	0.3188	0.7436	**0.0133**	0.4839
MC	2	0.9359	**0.0388**	**0.0467**	0.6911	0.6040
TRT*MC	4	0.7447	0.7035	0.7591	0.9765	0.8960
YR	1	**0.0172**	**0.0028**	**0.0083**	**0.0004**	0.4072
TRT*YR	2	0.6296	0.6821	0.6070	0.0825	0.6492
MC*YR	2	0.7566	0.2008	0.5054	0.5576	0.7220
TRT*MC*YR	4	0.6811	0.6576	0.8554	0.5631	0.8017

Table 3
Absolute density (stems ha^{-1}) of small seedlings (stems < 0.6 m tall) for each species group by year, treatment, and moisture class within the Daniel Boone National Forest, Kentucky. Values represent the mean (standard error). Means followed by the same letter are not significantly different within a given species group. *indicates a significant difference in small seedling density within the Subxeric moisture class between 2002 (4128 ± 554 ha^{-1}) and 2015 (5545 ± 294 ha^{-1}).

	Maple	Oak-Hickory	Other	Sassafras	Tolerant
Year					
2002	4872 (288)	4925^{A} (588)	2800 (439)	3865^{A} (431)	4338 (395)
2015	5259 (262)	7279^{B} (586)	3105 (488)	2775^{B} (387)	4026 (467)
Treatment					
FE	5326 (302)	5504 (855)	4099 (609)	3176 (610)	5581 (450)
FF	4938 (337)	6460 (898)	3225 (635)	3075 (511)	4349 (528)
LFF	4977 (363)	6250 (607)	1818 (324)	3650 (465)	2945 (398)
Moisture class					
Subxeric	4836^{*} (360)	7884^{A} (822)	1247^{A} (425)	3832^{A} (532)	3387 (423)
Intermediate	5200 (254)	7121^{A} (576)	2938^{B} (423)	4100^{A} (418)	4256 (442)
Submesic	5115 (414)	3397^{B} (420)	4461^{C} (557)	1995^{B} (465)	4793 (646)

Oak-Hickory seedling density on Subxeric and Intermediate sites averaged 1111 ha^{-1} and was significantly greater than on Submesic sites where large seedlings averaged only 257 ha^{-1}.

3.4. Small saplings

Regardless of frequency, fire had no significant impact on the density of small saplings in the Maple, Other, and Tolerant species group, however, significant increases in small sapling density between 2002 and 2015 suggests recruitment into the small sapling size class occurred regardless of treatment or moisture class (Fig. 4). Fire significantly affected the absolute density of small (stems $\geq$ 1.2 m tall and <3.8 cm dbh) Oak-Hickory saplings, and this effect varied by year (Table 2). In 2002, prior to treatment, small Oak-Hickory density averaged only 24 stems ha^{-1} across the FE, FF, and LFF treatments. Oak-Hickory small sapling density increased between 2002 and 2015 in both the FF and LFF treatments (Fig. 5a). However, by 2015, only the LFF treatment possessed small Oak-Hickory sapling densities in excess of that observed in the FE treatment, with small Oak-Hickory saplings averaging 45, 201, and 754 ha^{-1} in the FE, FF, and LFF treatments, respectively. Small Oak-Hickory sapling density varied across moisture classes, but only in 2015 (Table 2, Fig. 5b). In 2002, small Oak-Hickory saplings averaged 25 ha^{-1} on Subxeric, Intermediate, and Submesic sites. By 2015, small Oak-Hickory sapling density on Subxeric sites averaged 714 ha^{-1} and was significantly greater than on Submesic sites where small saplings averaged 125 ha^{-1}.

Fire significantly affected the absolute density of small Sassafras saplings, and this effect again varied by year (Table 2). In 2002, prior to treatment, small Sassafras sapling density averaged only 90 stems ha^{-1} across the FE, FF, and LFF treatments. For Sassafras small sapling density increased between 2002 and 2015 in both

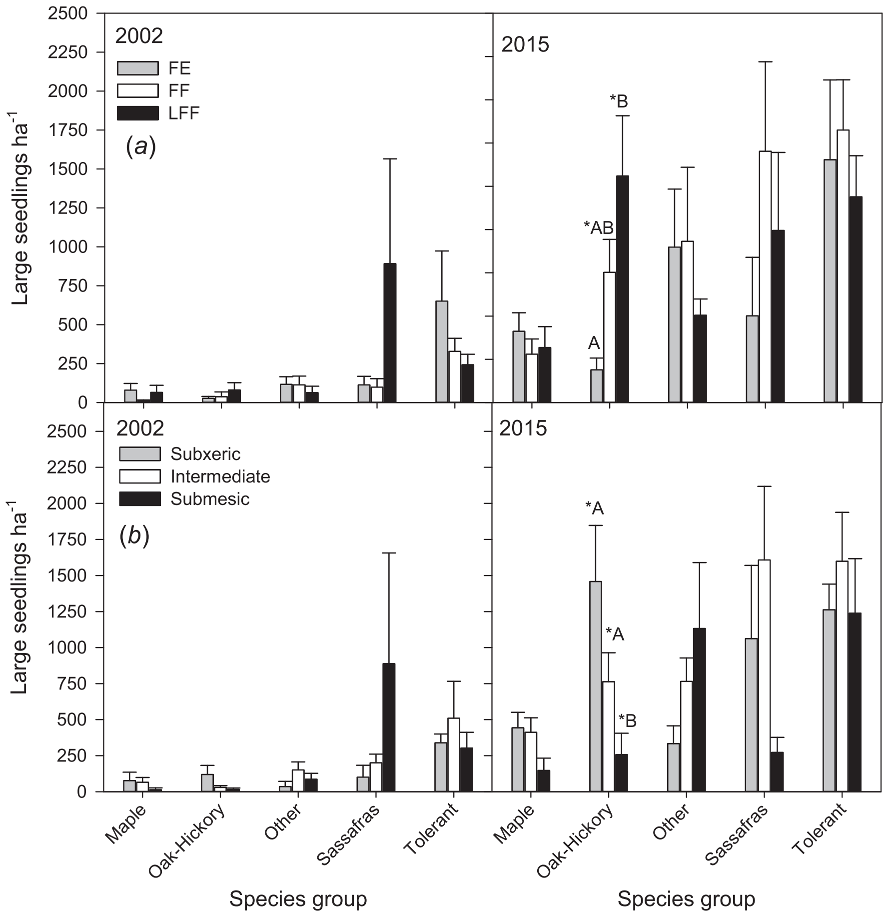

Fig. 2. Absolute density (stems ha^{-1}) of large seedlings (stems ≥ 0.6 m tall and <1.2 m tall) averaged (*a*) across moisture classes, and (*b*) across treatments by species group in 2002 and 2015 within the Daniel Boone National Forest, Kentucky. Means followed by similar letters are not significantly different among treatments or moisture classes within a given species group. Within a species group, *indicates a significant difference in large seedling density between years within a given treatment or moisture class.

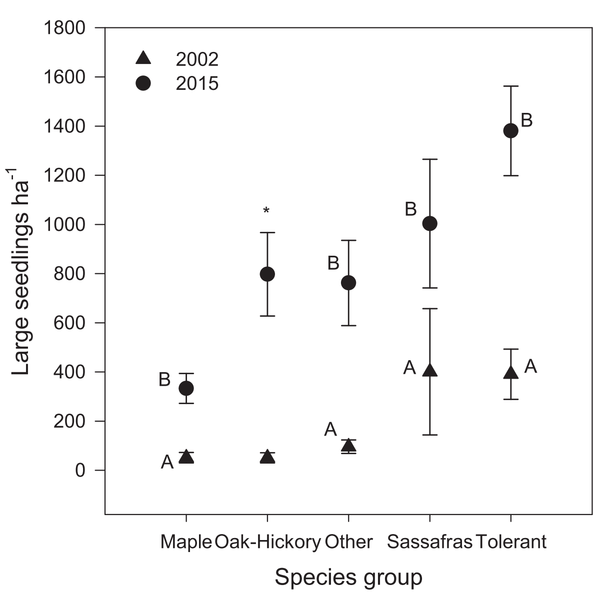

Fig. 3. Absolute density (stems ha^{-1}) of large seedlings (stems ≥ 0.6 m tall and <1.2 m tall) averaged across treatments and moisture classes. Means followed by the same letter are not significantly different within a species group. *indicates a significant treatment*year and moisture class*year (see Fig. 2).

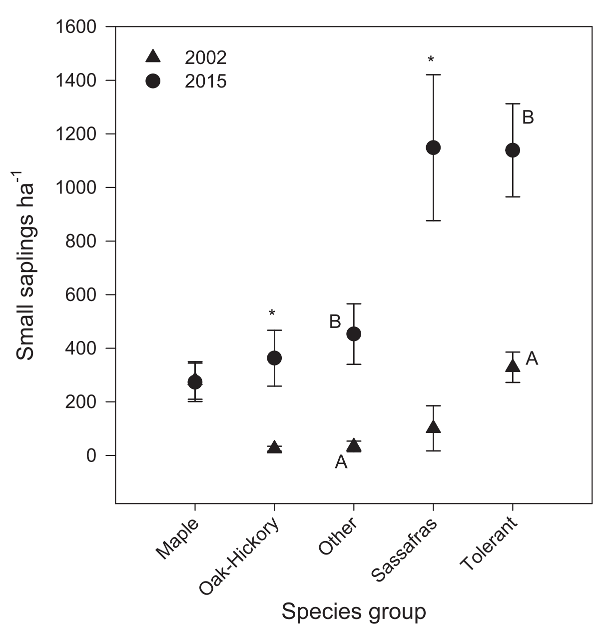

Fig. 4. Absolute density (stems ha^{-1}) of small saplings (stems ≥ 1.2 m tall and <3.8 cm dbh) averaged across treatments and moisture classes. Means followed by the same letter are not significantly different within a species group. *indicates a significant treatment*year and/or moisture class*year (see Fig. 5).

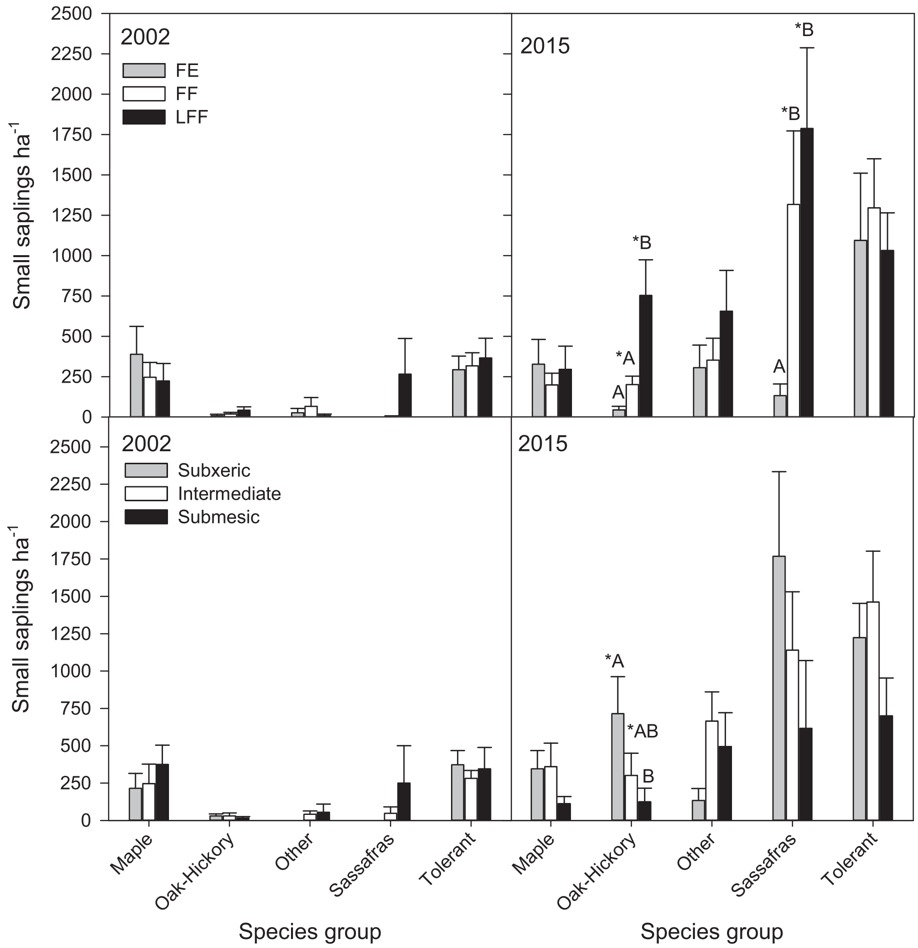

Fig. 5. (*a*) Absolute density (stems ha^{-1}) of small saplings (stems ≥ 1.2 m tall and <3.8 cm dbh) averaged (*a*) across moisture classes, and (*b*) across treatments by species group in 2002 and 2015 within the Daniel Boone National Forest, Kentucky. Means followed by similar letters are not significantly different among treatments or moisture classes within a given species group. Within a species group, *indicates a significant increase in small sapling density between years within a given treatment or moisture class.

the FF and LFF treatments (Fig. 5a). Small Sassafras saplings in both FF and LFF increased relative to the FE treatment, with small sapling density on average 11.7 times greater in the FF and LFF treatments than FE treatment.

Regardless of frequency, fire had no effect on the relative density of the Maple, Oak-Hickory, Other, and Tolerant species groups in the small sapling layer (Table 2). Only for Sassafras did relative density in the small sapling layer change, increasing significantly from 3% in the FE to an average of 23% in the FF and LFF treatments (Table 4). Irrespective of treatment and moisture class, relative density of Oak-Hickory, Other, and Sassafras species groups in the small sapling layer increased significantly between 2002 and 2015 (Table 4) relative to that of Maple which declined from 33% in 2002 to 12% in 2015. Relative density of Oak-Hickory and Other species groups in the small sapling layer varied across moisture classes, with relative density of Oak-Hickory greatest on Subxeric sites and lowest on Submesic sites (Table 4). In comparison, relative density of the other species group in the small sapling layer was greatest on Submesic and Intermediate sites and lowest on Subxeric sites.

Table 4
Relative density (%) of a given species group within the small sapling (stems ≥ 1.2 m tall and <3.8 cm dbh) by year, treatment, and moisture class within the Daniel Boone National Forest, Kentucky. Values represent the mean (standard error). Means followed by the same letter are not significantly different within a given species group.

	Maple	Oak-Hickory	Other	Sassafras	Tolerant
Year					
2002	33.2^{A} (6.4)	3.3^{A} (1.2)	3.2^{A} (1.7)	6.3^{A} (4.4)	49.8 (6.6)
2015	11.7^{B} (3.6)	8.4^{B} (1.8)	12.0^{B} (2.6)	27.4^{B} (5.5)	40.5 (5.3)
Treatment					
FE	35.0 (8.4)	2.4 (1.3)	6.1 (2.5)	2.5^{A} (1.5)	53.9 (7.9)
FF	21.6 (6.8)	4.7 (1.3)	7.8 (3.0)	20.6^{B} (7.4)	45.3 (6.4)
LFF	13.4 (5.0)	9.5 (2.4)	8.6 (3.2)	24.7^{B} (7.0)	38.2 (7.5)
Moisture class					
Subxeric	18.6 (5.8)	10.6^{A} (2.6)	1.4^{A} (0.8)	16.8 (6.2)	45.5 (7.1)
Intermediate	20.6 (5.6)	5.0^{AB} (1.7)	10.8^{B} (2.7)	16.3 (5.3)	47.3 (6.7)
Submesic	27.9 (8.9)	2.6^{B} (1.2)	9.5^{AB} (3.7)	17.6 (8.5)	42.4 (8.6)

4. Discussion

This study is one of only a few (e.g., Hutchinson et al., 2012a,b; Waldrop et al., 2016) to quantify the effects of repeated burns conducted at the landscape-level after a relatively long fire-free interval ($\geq$5 years) on the woody regeneration layer in mature, mixed-oak forests. Prior to and after the cessation of burning, the woody regeneration layer was dominated by species other than Oak-Hickory; a condition typical of mature second-growth upland hardwood forests in the Cumberland Plateau (Arthur et al., 1998; McEwan et al., 2005; Blankenship and Arthur, 2006; Hart and Grissino-Mayer, 2008). Furthermore, although Oak-Hickory seedlings were abundant, particularly on Subxeric and Intermediate moisture classes, the vast majority of seedlings were <0.6 m. Within the woody regeneration layer, large seedlings and small saplings, regardless of species, represent the individuals most likely to successfully compete (i.e., achieve presence in the dominant/co-dominant canopy layers) following overstory disturbance (Sander and Graney, 1992; Loftis, 1990a). For large seedlings and small saplings, we found partial support for our hypothesis (H1) that Oak-Hickory in the woody regeneration layer would increase in abundance in response to fire. However, we found the LFF treatment, not the FF treatment as hypothesized, provided the greatest benefit to Oak-Hickory. Relative to the FE treatment, we documented an increase of 1121 large Oak-Hickory seedlings ha^{-1} and 709 small Oak-Hickory saplings ha^{-1} in the LFF treatment, while large seedling and small sapling density remained similar between the FE and FF treatments. Data regarding the medium (i.e., 5 years) and long-term (i.e., >10 years) effects of landscape-level repeated burning on the woody regeneration layer in mixed-oak forests are sparse and results inconsistent across studies. In southern Ohio, Hutchinson et al. (2012a) observed three and five burns conducted over a 10-year period increased absolute and relative density of Oak-Hickory in the small sapling layer (stems >1.4 m tall and <3.0 cm dbh) three to four growing seasons after burning ceased. In contrast, two growing seasons after burning concluded, Blankenship and Arthur (2006) found the competitive status of sapling-sized oaks (stems > 50 cm tall and <2 cm dbh) in the forest understory had not improved over the course of nine years and three burns. In the southern Appalachians, Waldrop et al. (2016) found repeated burning (three burns conducted over a 12-year period) significantly increased the density of oak seedlings (<1.4 m tall) in the forest understory, however, the density of competitor species seedlings remained high (47%–340% greater than oak seedling density). The authors report similar results with mechanical thinning following by repeated burning suggesting herbicide application and/or growing season burning (Brose et al., 1999) may be necessary to reduce the abundance and sprouting of competitor species.

The failure of the FF treatment to promote recruitment of Oak-Hickory into large seedling or small sapling size classes despite the similarity of overstory, midstory, and large sapling density between the FF and LFF treatments (Arthur et al., 2015) combined with disparate results among repeated burn studies (e.g., Blankenship and Arthur, 2006; Hutchinson et al., 2012a) suggests the fire-free period, or antecedent periods between fires (*sensu* Arthur et al., 2015), plays an important role in Oak-Hickory seedling development and recruitment. In this study, post-treatment data were collected five and seven growing seasons after burning ceased in the FF and LFF treatments, respectively, suggesting differential effects of FF and LFF treatments on larger Oak-Hickory stems may be as much a function of the fire-free period specific to each treatment as fire frequency *per se*. Oaks display a conservative growth strategy whereby carbon is proportionally allocated to belowground versus aboveground growth (Kolb et al., 1990) which, coupled with dormant basal buds located below the soil surface, confers superior sprouting and growth following top-kill relative to mesophytic, shade-tolerant species (Brose et al., 2013). Despite these characteristics, high frequency fire that results in recurrent top-kill and sprouting can restrict seedling development into more fire-resistant size classes and eventual recruitment (Alexander et al., 2008; Peterson and Reich, 2008; Knapp et al., 2015). In comparison, fire regimes characterized by less frequent fire and relatively long fire-free periods permit the recovery of biomass and facilitate recruitment into larger, more fire-resistant and competitive size classes (Peterson and Reich, 2001). Once a pool of competitive oaks develop, Dey (2014) suggests a fire-fire period between 10 and 30 years will be required for recruitment into the midstory and overstory canopy layers. However, under an intact forest canopy fire-free periods as low as 14 years may also allow non-Oak-Hickory species, including red maple, sourwood, and blackgum, to develop into size classes resistant to future fire mortality (Harmon, 1984; Signell et al., 2005). In contemporary forests, there appears to be a trade-off between the need to control the density of non-Oak-Hickory competitors via frequent burning (e.g., Knapp et al., 2015) and the fire-free period essential to the post-fire recovery and recruitment of Oak-Hickory in the woody regeneration layer.

Critical to the recruitment of Oak-Hickory species in the woody regeneration layer following fire is the abundance and size of competing species. In this study, we found no support for our hypothesis (H2) that fire, and, more specifically frequent fire, would reduce the abundance of non-Oak-Hickory species in the woody regeneration layer. Regardless of size class, the FF and LFF treatments were ineffective at reducing the abundance of non-Oak-Hickory competitors. In fact, across treatments and moisture classes, absolute density of large seedlings and small saplings for all species groups other than Maple and relative density of all species groups other than the Tolerant group were significantly greater in 2015, five to seven growing seasons after burning ceased, than in 2002. The lack of treatment effects on small sapling-sized Maple and Tolerant species is likely related to the continued and often vigorous sprouting of top-killed stems in the large sapling and midstory layers in both burn treatments (Hutchinson et al., 2012a; Arthur et al., 2015). Although the increase in the absolute density of small Sassafras saplings observed in both the FF and LFF treatments was significant, intolerance of shade and relatively short lifespan (Burns and Honkala, 1990) suggest it will have minimal impact on the development and recruitment of both Oak-Hickory and non-Oak-Hickory species in the woody regeneration layer.

Fire behavior varies across a topographically complex landscape, with greater fire intensity occurring on poor quality, xeric locations (e.g., ridgetops, south-facing slopes) versus highly productive, mesic (e.g., coves, north-facing slopes) portions of the landscape (Elliott et al., 1999; Iverson et al., 2004). The effects of this variability in fire intensity often manifest in more pronounced changes in stand structure with decreasing productivity and moisture availability (e.g., Albrecht and McCarthy, 2006; Iverson et al., 2008). In our study, treatment effects, although variable across species groups and years, did not vary across moisture classes (i.e., no significant interaction between treatment and moisture class), providing no support for our hypothesis (H3) that changes in the abundance and composition of the woody regeneration layer, regardless of fire frequency, would be more pronounced on Subxeric versus Submesic sites (H3). Our results are in contrast to prescribed burning studies in mixed-oak forests in southern Ohio. For example, following thinning and repeated burning, Iverson et al. (2008) noted that changes in the abundance of seedlings (stems < 1.4 m tall) and small saplings (stems $\geq$ 1.4 m tall and <3.0 cm dbh) of red maple, yellow-poplar, oak and hickory, and sassafras were more pronounced on dry and intermediate sites than mesic sites after a two year (growing season) fire-free period. Similarly, in mixed-oak forests of southern Ohio, Hutchinson et al. (2012a) documented that positive effects of repeated burning, after a three or four year fire-free period, on the absolute and relative abundance of oak and hickory in the small sapling (stems 1.4 m tall to <3.0 cm dbh) layer were limited to dryer portions of the landscape, with no positive effects observed on mesic sites. Again, however, differences in fire-free periods between the current study and others (e.g., Iverson et al., 2008; Hutchinson et al., 2012a) are a confounding factor limiting direct comparison of results among studies. In this study, the expert system used to differentiate moisture classes, which was based on pre-treatment species composition, indicated clear discrimination between Subxeric and Submesic plots, with substantial overlap observed between Intermediate plots and Subxeric and Submesic plots (McNab et al., 2007). This coarse filter approach to assessing moisture/productivity gradients may explain, in part, the lack of interaction between moisture class and burn treatment. A more direct and objective method of assessing moisture/productivity that uses a combination of topographic (i.e., slope, aspect, curvature) and soils (i.e., water holding capacity) data (e.g., the Integrated Moisture Index; Iverson et al., 1997) may better quantify landscape-level moisture/productivity gradients and, therefore, increase sensitivity to burn treatments (Iverson et al., 2008).

5. Conclusions

Oak regeneration, or more specifically, oak recruitment, from the woody regeneration layer into the subcanopy, midstory, and, eventually, canopy layers continues to be problematic across the eastern US (Dey, 2014; Lafon et al., 2017). There is growing recognition that frequent disturbance, including fire, was a critical force shaping pre-European and modern day structure and composition (Abrams, 1992; McEwan et al., 2011). Changes in land-use have resulted in disturbance regimes characterized by low frequency and low severity disturbance events (Buchanan and Hart, 2012) and, correspondingly, forest structures less conducive to the sustained recruitment of Oak-Hickory species across the landscape (Hart et al., 2012). Although recent research efforts have focused on fire frequency as a primary factor controlling woody vegetation response to prescribed burning, the results of our study suggest the intricate interactions of fire frequency and corresponding fire-free periods may be more of a factor controlling the abundance and composition of the woody regeneration layer following burning than simply the number of burns. In addition to the interplay between fire frequency and fire-free periods, there is increasing recognition of the role the seasonality of burning may have on the composition of the woody regeneration layer in oak-dominated forests. A meta-analysis by Brose et al. (2013) suggests that growing season burns conducted under an intact canopy actually increases mortality of Oak-Hickory in the woody regeneration layer relative to mesophytic competitors. In contrast, under reduced canopy cover, the authors report oak survival as well as relative abundance in the woody regeneration layer is greater following growing versus dormant season burning. Clearly, the factors associated with the reintroduction of fire to long undisturbed oak forests are innumerable, and the potential for interactions among abiotic and biotic factors great.

At our study sites, Arthur et al. (2015) found both FF and LFF treatments were effective at reducing density in the sapling and midstory layers, although overstory density remained similar to unburned stands. High overstory density, particularly on Submesic portions of the landscape (Arthur et al., 2015), will likely restrict recruitment of the large Oak-Hickory and/or small Oak-Hickory saplings that developed in response to the LFF treatment and promote the continued development of non-Oak-Hickory competitors in the forest understory. In comparatively dry oak forests of the Ozark Highlands, Larsen et al. (1997) found overstory (stems $\geq$ 15 cm dbh) basal area as low as 6.5 $m^2\,ha^{-1}$ reduced the probability of adequate oak seedling stocking. Similarly, in south central Pennsylvania, Signell et al. (2005) noted the development and recruitment of oak into the sapling (>1.45 m tall and <7.62 cm dbh) size class became significantly restricted when overstory and understory (i.e., suppressed trees) density exceeded 400 and 200 trees ha^{-1}, respectively. In old-growth oak forests, stand reconstruction studies suggest fire interacted with canopy-reducing disturbance events to facilitate the development and recruitment of oak across the landscape (Rentch et al., 2003a; b). Correspondingly, in contemporary secondary mixed-oak forests, Hutchinson et al. (2012b) observed significantly more abundant large oak regeneration (stems $\geq$ 0.3 m tall and <3.0 cm dbh) in repeatedly burned versus unburned stands following the natural canopy gap creation, presumably due to increased light levels in the forest understory subsequent to the elimination of shade-tolerant species in midstory (stems 3–20 cm dbh) prior to canopy gap formation. It is becoming clear that to develop large, competitive Oak-Hickory seedlings/saplings in long undisturbed forest stands in a timely manner, prescribed burning must be accompanied by reductions in canopy cover via natural (Hutchinson et al., 2012b) or silvicultural (Brose et al., 1999a, 2013; Brose, 2010) processes. In our study, it remains uncertain whether the large seedlings and small saplings in the Oak-Hickory group observed in the LFF treatment will be sustained in the long-term as sprouting from top-killed trees remains vigorous (Arthur et al., 2015) and the relative density of non-Oak-Hickory competitors remains high. Similarly, it is unclear whether additional years after cessation of fire in the FF treatments will lead to increases in seedling density. Therefore, should canopy disturbance(s) occur, it is uncertain whether the Oak-Hickory will outcompete the co-occurring competitor species also capable of responding positively to decreased canopy cover (e.g., Tift and Fajvan, 1999).

The 80+ years of fire exclusion and limited disturbance in the stands utilized in this study facilitated the development of dense regeneration, sapling, and midstory layers dominated by shade-tolerant, mesophytic species (Arthur et al., 2015). It appears that dormant season fire, even applied frequently, is ineffective at controlling the density and relative abundance of non-Oak-Hickory species in the woody regeneration layer. Additional treatments including herbicide application of non-Oak-Hickory competitors and/or additional prescribed burns conducted during the growing season may be necessary to reduce the abundance of non-Oak-Hickory competitors in the woody regeneration layer and increase the likelihood of Oak-Hickory recruitment should natural release events occur (Hutchinson et al., 2012b). In the FF treatment where the density of small Oak-Hickory saplings remains similar to unburned areas and in Submesic areas of the LFF treatment, where large Oak-Hickory seedling and small Oak-Hickory sapling density remains low, additional burning during the growing season coupled with silvicultural treatments, such as the oak shelterwood method (Loftis, 1990b), the shelterwood/burn technique (Brose et al., 1999a; b), or post-disturbance release burning (Brose, 2014; Brose et al., 2014) may be necessary to increase regeneration potential and ensure recruitment of Oak-Hickory into the canopy over the long-term.

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