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Long-term (13-year) effects of repeated prescribed fires on stand structure and tree regeneration in mixed-oak forests

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ABSTRACT

The survival and growth of oak advance regeneration is often limited by shade-tolerant species that are abundant in the understory of oak stands. Evidence of historic burning has prompted the use of prescribed fire as a tool to improve the competitive status of oak regeneration in mature stands. A primary shortfall of fire effects research in oak forests has been a lack of long-term studies on the effects of multiple fires. Here we describe the effects of repeated fires on stand structure and tree regeneration over a 13-year period in mature mixed-oak forests located in southern Ohio, USA. Three stands were burned 3–5 times from 1996 to 2005 with low-intensity dormant-season fires, and two stands remained unburned. Woody vegetation was sampled periodically on nine 0.125 ha plots per stand. Plots were located across the upland landscape and were characterized by an Integrated Moisture Index. Fire altered stand structure by reducing the density of large saplings (3.0–9.9 cm DBH) and midstory trees (10–25 cm DBH) by 76% and 34%, respectively. Fire had little impact on trees >25 cm DBH. Small saplings (1.4 m tall to 2.9 cm DBH) were dynamic over time on dry plots that were burned. After being repeatedly topkilled from year 1–8, the small sapling layer had redeveloped on dry burned plots by year 13 and species composition had shifted from dominance by shade-tolerant species to a more equal distribution of shade-tolerants, oaks + hickories, and sassafras. The density of oak + hickory and sassafras advance regeneration (stems 30 cm tall to 2.9 cm DBH) was significantly greater on burned plots than on unburned plots in year 13, though variability among plots was high. Advance regeneration of shade-tolerant species was equally abundant on burned and unburned plots. Density of oak + hickory advance regeneration in year 13 was positively related to its weighted frequency (a surrogate for size and abundance) in year 0 ($r^2 = 0.67$, $p < 0.0001$) and inversely related to stand density ($r^2 = 0.33$, $p < 0.0001$) and canopy cover ($r^2 = 0.31$, $p < 0.0001$), both of which were reduced by fire. Although oak + hickory advance regeneration was more abundant on burned plots, we conclude that other methods (e.g., herbicide, partial cutting) are necessary to further reduce stand density and promote the development of larger oak + hickory regeneration, particularly on mesic sites.

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1. Introduction

There is increasing evidence that forests in the Central Hardwoods Region (CHR) of the eastern United States are shifting towards less dominance by oaks (*Quercus* L.) (Lorimer, 1984; Abrams, 2003; Widmann et al., 2009). The successful regeneration of oak forests depends on the presence of adequate densities of competitive oak seedlings (advance regeneration) before a canopy disturbance (Crow, 1988; Loftis, 2004). However, many factors, which vary at regional and local scales, contribute to the poor development of oak advance regeneration (Lorimer, 1993). Arguably, the most important factor that limits oak regeneration in many areas is the increasing abundance of shade-tolerant species (e.g., red maple [*Acer rubrum* L.], sugar maple [*A. saccharum* Marsh.]) in the midstory and understory, which reduces light availability to the forest floor (Lorimer et al., 1994; Abrams, 1998; Fei and Steiner, 2007). Poor oak regeneration occurs after a disturbance when oak seedlings are too small and/or too sparse to compete successfully with established shade-tolerant species and/or newly-established but fast-growing shade-intolerant species such as yellow-poplar (*Liriodendron tulipifera* L.) and sweet birch (*Betula lenta* L.) (Loftis, 1990; Abrams and Nowacki, 1992; Schuler and Miller, 1995; Jenkins and Parker, 1998). Across much of the CHR, the “oak regeneration problem” is one of the most important forest management issues today (Yaussy et al., 2008).

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The abundance of shade-tolerant competitors in oak forests has been linked to changing disturbance regimes, especially the reduced frequency of fire since organized fire control was instituted in the early 20th century (Abrams, 1992). In the last two decades a better understanding of the importance of prehistoric and historic burning in the CHR has emerged. Evidence from historical accounts, palynology, archaeology, original land surveys, and dendrochronology indicate that anthropogenic fire has been associated with the widespread dominance of oak ecosystems in the CHR for several millennia (e.g., Whitney, 1994; Delcourt et al., 1998; Guyette et al., 2002; Fesenmyer and Christensen, 2010). Dendrochronology studies have also provided evidence linking the cessation of periodic fires to the establishment of non-oak species in oak forests (Shumway et al., 2001; Hutchinson et al., 2008).

Oaks and the ecologically-similar hickories (*Carya* Nutt.) possess a suite of attributes in all life-stages that should confer a competitive advantage in a regime of periodic fire, including relatively thick bark (Hare, 1965; Hengst and Dawson, 1994), efficient wound compartmentalization (Smith and Sutherland, 1999), dormant root collar buds located deeper in the soil than those of most competing species (Brose and Van Lear, 1998), and the capacity to sprout repeatedly from these dormant buds using carbohydrate reserves achieved through "root-centered" growth (Merz and Boyce, 1956). For reviews of oaks' adaptations to fire and other disturbances, see Johnson et al. (2009) and Dey and Fan (2009).

The increasing awareness of fire's historical role and the fire-adapted traits of oaks have led to the increased use of prescribed fire in oak woodlands and forests on public lands. Burning in mature oak forests has yielded a variety of outcomes with respect to oak regeneration. Prescribed fire has been shown to increase the competitive status of oak regeneration in some studies (Maslen, 1989; Barnes and Van Lear, 1998; Fan et al., 2012) but other research has found that prescribed fire can decrease oak's competitive position (Loftis, 1990; McGee et al., 1995; Blankenship and Arthur, 2006). This contrast is not surprising given the wide range of stand conditions and fire application in those and other studies (Brose et al., 2006). In addition, a shortfall of the research to date has been a lack of long-term studies on the effects of repeated prescribed fires on forest structure and tree regeneration in oak forests.

In 1995, a study was established in southern Ohio to document the long-term effects of repeated prescribed fires on mature oak forest ecosystems (Sutherland and Hutchinson, 2003). We hypothesized that, over the long-term, repeated low-intensity fires would reduce stem density in the midstory and understory, which were dominated by shade-tolerant species. We also hypothesized that repeated fires would increase the competitive status of oak and hickory advance regeneration due to their sprouting capacity after fire and increased light to the forest floor. A better understanding of how mature oak forests respond to multiple prescribed fires will help managers in their quest to sustain this forest type throughout eastern North America.

Fire effects on belowground processes and understory vegetation have been reported previously (e.g., Dress and Boerner, 2001; Boerner et al., 2004; Hutchinson et al., 2005a). Hutchinson et al. (2005b) described changes in forest structure from years 0 to 7 and the abundance of advance regeneration in year 7. In this study, after one additional fire in each burn unit, we describe the effects of 3–5 prescribed fires on the structure and composition of the overstory, midstory, and sapling layers through year 13, as well as the composition and abundance of tree regeneration on burned and unburned sites in year 13. By providing a longer-term analysis, after a greater post-fire interval, our goal was to document additional changes in forest structure and to track the redevelopment of the understory after the cessation of burning. A companion study (Hutchinson et al., 2012) documented tree regeneration in burned and unburned canopy gaps on these same study sites, also in year 13, but employed different sampling locations, centered in canopy gaps.

2. Methods

2.1. Study area description

This study was conducted in Vinton County, OH, on the Vinton Furnace State Experimental Forest (VFSEF; 39°11′N; 82°22′W). The VFSEF lies within the unglaciated Allegheny Plateau of southern Ohio. Topography is a dissected plateau consisting of narrow ridges and steep slopes. Elevation ranges from 220 to 300 m. Soils are mapped as the Steinsburg–Gilpin Association on ridges and upper slopes and the Germano–Gilpin Complex on lower slopes (Boerner and Sutherland, 2003). These soils are silt and sandy loams formed in residuum from sandstone and shale parent material. Consequently, soils are acidic, moderately fertile, and well-drained. Depth to bedrock averages 130 cm and typically ranges from 50 to 225 cm (Matthew Dickinson, US Forest Service, unpublished data). Oak site index$_{age50}$ ranges from approximately 17 m on ridgetops and upper south-facing slopes to 25 m on lower north-facing slopes (Carmean, 1965). Mean annual temperature is 11.3 °C; precipitation averages 1024 mm and is distributed evenly throughout the year.

Original land surveys in the region (ca. 1800) indicate that oaks dominated upland forests prior to Euro-American settlement (Beatley and Bartley, 1959; Dyer, 2001). In the mid-to-late 1800s, forests were clearcut to provide charcoal for iron production. Fire history studies on the VFSEF indicate a fire return interval of 6–9 years from ca. 1875–1935 but thereafter fires essentially ceased due to effective fire control policies (Sutherland, 1997; McEwan et al., 2007; Hutchinson et al., 2008).

Table 1
Pre-treatment attributes (mean [range]) for the two unburned (UB) and three burned (3X, 5X) stands.

Stand	Area (ha)	Overstory[a]		Saplings[b]		Seedlings[c]
		Basal area (m^2 ha^{-1})	Oak + hickory basal area (%)	Density, stems (ha^{-1})	Shade-tolerant density (%)	Oak + hickory density, stems (ha^{-1})
AR/UB	24	25.9 ± 1.01 (21.1–31.1)	82.6 ± 3.9 (70.5–100)	2005 ± 85.0 (960–3456)	87.3 ± 7.7 (26.2–100)	17222 ± 7400 (0–70,000)
WR/UB	20	25.9 ± 0.85 (21.4–28.7)	81.8 ± 3.7 (62.4–96.4)	1668 ± 60.9 (1056–2433)	96.4 ± 1.5 (84.7–100)	5000 ± 1102 (0–10,000)
AR/3X	24	27.2 ± 1.19 (22.1–33.3)	90.5 ± 2.2 (81.9–99.0)	1892 ± 55.5 (576–3584)	95.8 ± 1.5 (86.4–100)	10556 ± 2422 (0–22,500)
AR/5X	32	28.4 ± 1.45 (21.2–35.2)	77.0 ± 7.2 (37.8–95.6)	2140 ± 72.7 (864–4570)	93.9 ± 2.0 (81.8–100)	6667 ± 2796 (0–27,500)
WR/5X	31	23.5 ± 1.32 (17.4–28.6)	82.2 ± 5.0 (46.0–98.6)	1788 ± 60.8 (800–3008)	77.8 ± 5.5 (44.4–98.1)	9444 ± 3027 (0–27,500)

Note: Data were collected in 1995 on nine 0.125 ha plots per stand.
[a] Calculated from trees ⩾10 cm DBH.
[b] Stems 1.4 m tall to 9.9 cm DBH.
[c] All stems <1.4 m tall.

In 1995, prior to the initiation of fire treatments, the overstory was dominated by white oak (*Q. alba* L.), black oak (*Q. velutina* Lam.), chestnut oak (*Q. prinus* L.) and hickories (*Carya* Nutt.) (Table 1). Shade-tolerant species such as red maple, blackgum (*Nyssa sylvatica* Marsh. var. *sylvatica*), American beech (*Fagus grandifolia* Ehrh.), and flowering dogwood (*Cornus florida* L.) dominated the sapling layer. The density of oak + hickory seedlings was highly variable across the landscape (Table 1).

2.2. Distribution of treatment units and plots

Originally, the study contained four 75 ha replicate sites, Arch Rock and Watch Rock on the VFSEF, and two additional sites located 50 and 70 km to the south in Lawrence County, on the Wayne National Forest, Ironton Ranger District (Sutherland et al., 2003). Here we report only on the two VFSEF sites, as logistical and funding limitations prevented the maintenance of the Lawrence County sites. Each site was divided into three units of 25–30 ha and randomly assigned to one of three fire treatments. For the initial 5 years of the study, the three fire treatments were frequent burn (four fires in 4 years), periodic burn (two fires in 4 years), and an unburned control.

In 1994, nine 0.125 ha vegetation sampling plots were established in each treatment unit (Fig. 1). These plots were distributed across the treatment units to capture the full range of upland soil moisture conditions estimated by the Integrated Moisture Index (IMI, Iverson et al., 1997). IMI is a geographic information system-derived index (30-m resolution) that estimates long-term soil moisture availability based on topography and soils. The IMI for each 30-m pixel ranges from 0 (driest) to 100 (wettest) and comprises four weighted components, a slope-aspect shading index ("hillshade", 40% weighting), the cumulative flow of water downslope ("flow accumulation", 30%), soil water-holding capacity (20%), and landscape curvature (10%). An IMI value was calculated for each plot as the average IMI score among the four plot corners and two midpoints (see Iverson and Prasad, 2003). IMI values for the 45 plots in this paper ranged from 22.2 (driest) to 78.8 (wettest). Plots were also classified into two categories based on IMI: plots with IMI <45 were classified as dry ($n = 24$) and plots with IMI >45 were classified as mesic ($n = 21$).

2.3. Pre-burn data collection

Woody vegetation was inventoried in 1995 (hereafter year 0), prior to fire treatments. In each 0.125 ha plot, all trees ⩾10 cm diameter at 1.37 m above the ground (DBH) were tagged, identified to species, measured for DBH to the nearest 0.1 cm, and classified as living or dead. Saplings (stems 1.4 m tall to 9.9 cm DBH) were tallied by species and size class in one-quarter (312.5 m^2) of the

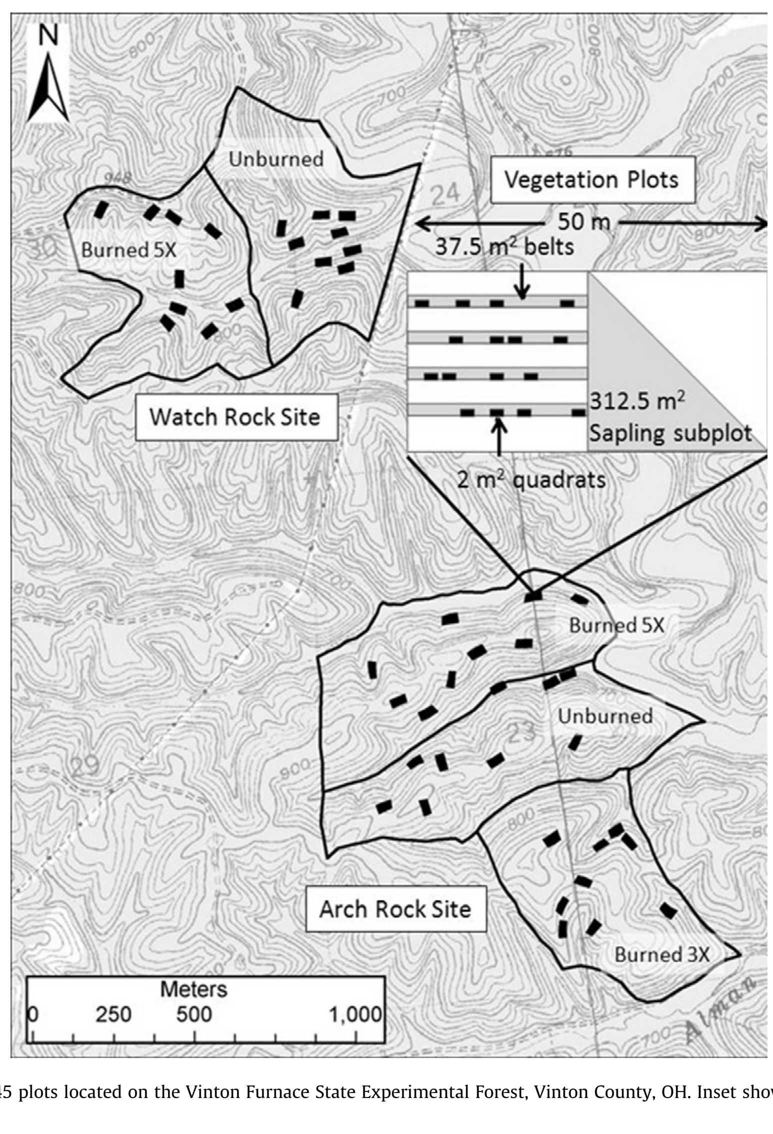

Fig. 1. Map of the five stands and 45 plots located on the Vinton Furnace State Experimental Forest, Vinton County, OH. Inset shows the sampling design within a plot.

plot (Fig. 1). Size classes for saplings were 1.4 m tall to 2.9 cm DBH (small) and 3.0–9.9 cm DBH (large).

Tree seedlings (all stems <1.4 m tall) were originally tallied on two 2-m^2 quadrats within the 0.125 ha plot. However, these subplots proved inadequate to capture the abundance of larger stems (>30 cm tall) by species; data collection on these subplots was discontinued and these data are not used for analyses in this paper. To better understand the composition and abundance of small and larger tree seedlings by species prior to treatments, we used frequency data that were collected for all vascular plant species in year 0 (see Hutchinson et al., 2005a). In each of sixteen 2-m^2 quadrats located on one-half of the 0.125 ha plot, the presence of tree seedlings was recorded by species in two size classes: <30 cm tall (small) and >30 cm tall (large) (Fig. 1). The quadrats were distributed along four 25-m transects that were spaced 5 m apart.

2.4. Prescribed fires

Thirteen prescribed fires were conducted from 1996 (year 1) to 2005 (year 10) by personnel of the Ohio Division of Forestry and the Wayne National Forest (Table 2). In two of the burn units (Arch Rock 5X and Watch Rock 5X), annual fires were applied from years 1–4 and then an additional burn was conducted in year 9, for a total of five burns. In the third burn unit (Arch Rock 3X), fires were applied in years 1, 4, and 10. All but one fire occurred from 21 March to 21 April, in the spring dormant season, when leaves of overstory and understory trees had not yet expanded. A single fire was applied in the fall dormant season. Prescribed fires were ignited primarily with strip head-fires. Although fires were generally low intensity, with flame lengths <1 m, most of the landscape was burned, typically >85% of the burn unit during each fire.

2.5. Post-burn data collection

From 1996 (year 1) to 2008 (year 13), we re-inventoried the sampling plots on a periodic basis as budget and time allowed. Not all variables were remeasured at the same intervals. The overstory trees were remeasured in years 1, 4, 7, and 13. Saplings were re-inventoried annually from years 1 to 4 and again in years 7 and 13. In year 13, multi-stemmed sprouts >140 cm tall that had originated from topkilled stems >5 cm basal diameter were also recorded in the sapling subplots. For tree seedlings >30 cm tall, we recorded abundance by species in years 7 and 13 along the same four transects that were used to record species' presence in 1995; these larger seedlings were recorded in 1.5 × 25 m belt transects (150-m^2 area sampled per plot) (Fig 1). Size classes were 30.0–59.9 cm tall and 60.0–139.9 cm tall. Multiple sprouts from the same rootstock were recorded as one individual seedling.

Canopy openness for each plot was estimated by hemispheric photography. Photographs were taken in years 0, 1, 2, 4, and 13, from the center of each 0.125 ha plot. Color slide photographs were taken in years 0–2 and digital photographs were taken in years 4 and 13. The software GLA (Gap Light Analyzer, Version 2.0, Simon Fraser University, Burnaby, BC, and the Institute of Ecosystem Studies, Millbrook, NY) was used to calculate the percentage of open sky from the photographs.

Table 2
Dates (month/day) of the 13 prescribed fires conducted in three burn units.

Stand	Area (ha)	1996	1997	1998	1999	2004	2005
Arch Rock 5X	32	4/19	4/2	4/6	3/26	4/17	
Arch Rock 3X	24	4/18			3/26		4/15
Watch Rock 5X	31	4/21	4/3	4/6	3/27	11/9	

2.6. Data analyses

The study was originally designed with the four study areas as replicate blocks. However, because the two Lawrence County sites were discontinued after year 7, the statistical approach has been adjusted. In this paper the plots are treated as the experimental units and we use a regression (analysis of covariance, ANCOVA) approach. This approach is justified because the plots are: (1) relatively large (0.125 ha), (2) spatially distinct (most plots are more than 50 m from the nearest neighbor plot), and 3) are distributed across a relatively wide range of topographic conditions, which gives rise to significant variation in environmental conditions, vegetation, and fire behavior among plots within stands. This statistical approach limits our level of inference to the VFSEF. We focus our statistical analyses on year 0 (pre-burn) and year 13 conditions in five of the six units at the VFSEF: the two unburned units and the three burn units that were burned a minimum of three times between years 1 and 10 (Table 2). An additional burn unit (Watch Rock periodic) is not included in our analyses because only two fires were applied, and the first fire in year 1 failed to burn several plots. Previous analyses showed few differences in fire effects between the periodic and frequent burn treatments (Hutchinson et al., 2005b). Therefore, in this paper we classify plots as simply "burned" (n = 27 plots in 3 units) or "unburned" (n = 18 plots in 2 units).

Generalized linear mixed models were used to test for significant effects of fire on several measures of forest structure, the density of small saplings, the relative density of oak + hickory small saplings, and the density of advance regeneration for several common species/groups, in year 13 (SAS, Version 9.2, PROC GLIMMIX, SAS Institute, Inc., Cary, NC). In the models, site (Watch Rock or Arch Rock) was a random effect and fire (burned or unburned) was a fixed effect. These models represented a completely randomized design that incorporated random site effects. The covariate was the value of the dependent variable in year 0. However, for the models of advance regeneration density by species/group in year 13, the covariate was the weighted frequency of the species/group in year 0. The weighted frequency, calculated from data collected in the sixteen 2-m^2 quadrats, was used in the analysis because year 0 density data were inadequate (many plots with zero density). The weighted frequency for a species/group emphasized the importance of larger seedlings (e.g., see Marquis and Bjorkbom, 1982; Brose et al., 2008) and was calculated as the sum of the frequency of small seedlings (<30 cm tall) and frequency of large seedlings (>30 cm tall) multiplied by three. The 3X weighting for the frequency of larger seedlings in year 0 was selected because it was more strongly correlated with year 13 density of larger seedlings than other weightings (2X, 4X, 5X). For example, if small oak + hickory seedlings were present in 14 quadrats and large oak + hickory seedlings were present in 8 quadrats, the weighted frequency was calculated as $(14 \times 1) + (8 \times 3) = 38$.

The ANCOVA models were run in three steps. Step 1 tested whether the regression slopes were linear and significant. Step 2 tested whether the slopes for burned and unburned plots were parallel. Depending on the outcome of step 2, a final model (step 3) for parallel or unequal slopes was run. The normal distribution was specified for the following dependent variables: tree basal area (BA), overstory density and midstory density (default link function = identity). The gamma distribution (default link function = log) was specified for all other dependent variables, which exhibited a skewed-to-the-right distribution. The KENWOODROGER method was used to calculate the denominator degrees of freedom for tests of fixed effects.

Several ANCOVA models were run on a subset of the 45 plots. The model for sassafras (*Sassafras albidum* (Nutt.) Nees) density in year 13 did not converge when all 45 plots were included, due to zero density on nearly one-half of plots. The final ANCOVA model for sassafras density was run on the 27 plots (7 unburned plots, 20 burned plots) in which sassafras was present in year 13. Also because the density of stems in the small sapling size class was very low on mesic burned plots in year 13, the ANCOVA model for the relative density of small oak + hickory saplings was run only on plots classified as dry (IMI <45; $n = 24$).

Simple linear regression analysis was used to illustrate the relationship between year 0 weighted frequency and year 13 advance regeneration density for the oak + hickory group. We also used simple linear regression to determine which factors were most strongly related to the density of oak + hickory advance regeneration in year 13 (SAS Enterprise Guide 4.2). Independent variables were 1) weighted frequency oak + hickory in year 0, large sapling density in year 13, stand density in year 13% open sky in year 13, and IMI.

3. Results

3.1. Fire effects on forest structure

ANCOVA indicated that BA was significantly lower on burned plots (LS mean = 24.6 ± 0.7 m^2 ha^{-1}) than on unburned plots (LS mean = 28.7 ± 0.9 m^2 ha^{-1}) in year 13 ($F_{1,42} = 13.6$, $p < 0.001$; Fig. 2a). BA decreased by only 4.2% on burned plots from year 0 to 13 but simultaneously increased by 10.1% on unburned plots (Table 3). The density of larger overstory trees (>25 cm DBH) decreased by 9.6% on burned plots and by 3.5% on unburned plots from year 0 to 13. There was not a significant difference in overstory density between burned (LS mean = 169 ± 5.3 trees ha^{-1}) and unburned (LS mean = 159 ± 4.8 trees ha^{-1}) plots in year 13 ($F_{1,15.4} = 2.39$, $p = 0.074$; Fig. 2b). Fire had a greater effect on the midstory strata as the density of trees 10–25 cm DBH was reduced 34.0% on burned plots and increased slightly (0.7%) on unburned plots, from year 0 to 13. In year 13, the density of midstory trees was significantly lower ($F_{1,20.2} = 22.4$, $p < 0.001$) on burned plots (LS mean = 126 ± 9.5 trees/ha) than on unburned plots (LS mean = 196 ± 11.2 trees/ha) (Fig. 2c). Among the three burned stands, Arch Rock 3X exhibited the largest mean reductions in BA (−10.7%), overstory density (−15.7%), and midstory density (−47.5%), indicating greater fire intensity in that unit. Compositional changes in the midstory were not large. On control units, shade-tolerant species comprised 60% of trees in year 0 and 74% of trees in year 13; on burn units, 51% of midstory trees were shade-tolerant in year 0 and 58% of trees were shade-tolerant in year 13.

In year 0, 92% of large saplings (3.0–9.9 cm DBH) were shade-tolerant and the four most abundant species were red maple, blackgum, American beech, and flowering dogwood. The mean density of large saplings was reduced by 75.6% on burned plots by year 13 (Table 3), and was significantly lower ($F_{1,13.4} = 70.6$, $p < 0.001$) on burned plots (LS mean = 128 ± 41.5 stems ha^{-1}) than on unburned plots (LS mean = 539 ± 46.9 stems ha^{-1}) (Fig. 2d). On unburned plots, large sapling density increased slightly (4.2%) from

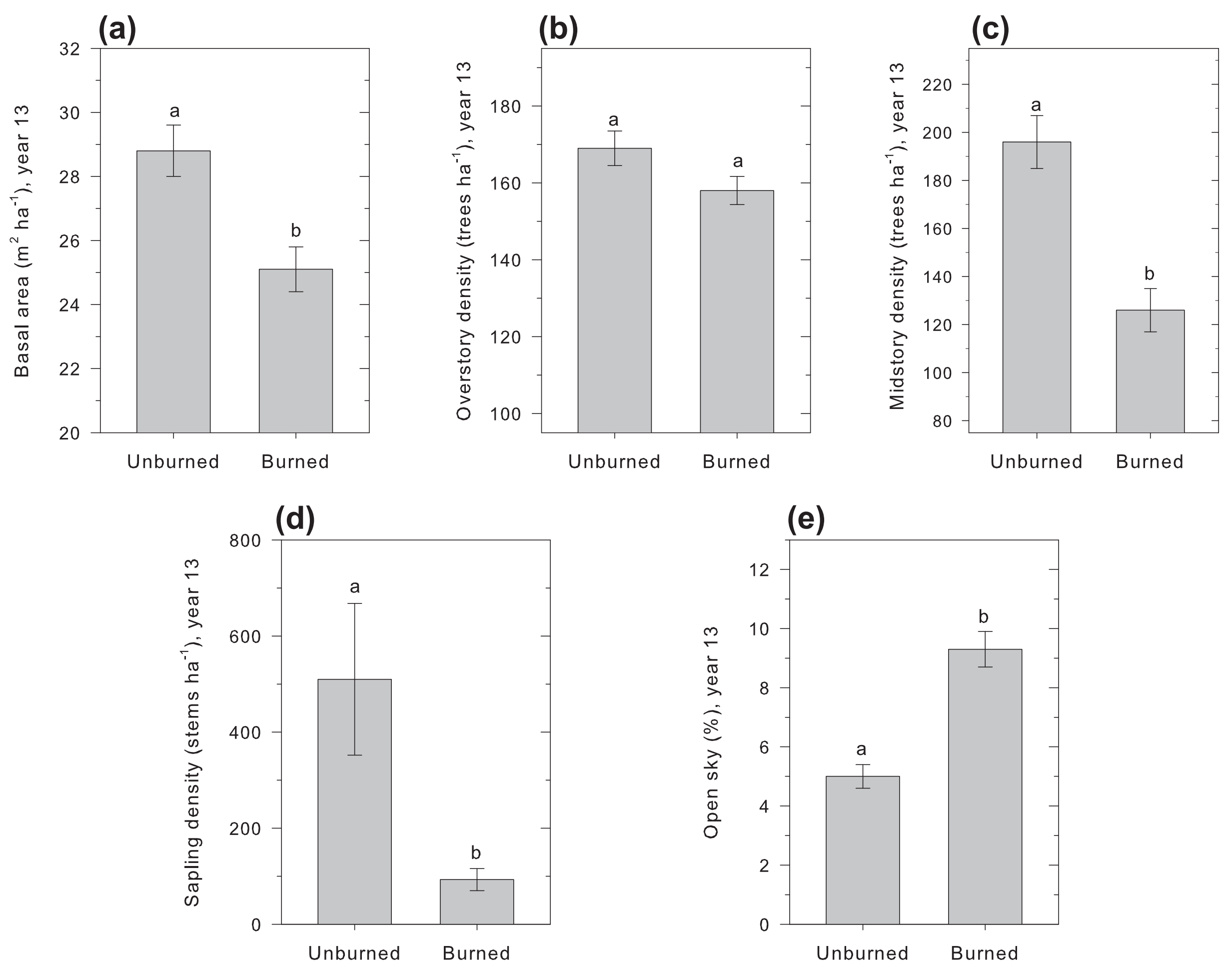

Fig. 2. Results of ANCOVA for structural attributes in year 13: (a) tree basal area, (b) overstory density (trees >25 cm DBH), (c) midstory density (trees 10–25 cm DBH), (d) large sapling density (stems 3.0–9.9 cm DBH), and (e) open sky. Bars represent adjusted LS means (±S.E.). Different letters above the bars indicate significant differences between burned and unburned plots.

Table 3
Mean values (±1 standard error) for stand structure variables in year 0 (1995) and year 13 (2008), and % change over that time period, in two unburned units and three burned units. Data were collected on nine 0.125 ha plots per unit.

Variable	Year % Change	Arch Unburned $n = 9$	Watch Unburned $n = 9$	Arch 3X burn $n = 9$	Arch 5X burn $n = 9$	Watch 5X burn $n = 9$	Unburned All $n = 18$	Burned All $n = 27$
Tree basal area, $m^2\ ha^{-1}$ (trees ⩾10 cm DBH)	Year 0	25.9 ± 1.0	25.9 ± 0.8	27.2 ± 1.2	28.4 ± 1.5	23.5 ± 1.3	25.9 ± 0.6	26.4 ± 0.8
	Year 13	28.8 ± 1.3	28.2 ± 1.0	24.3 ± 1.8	28.8 ± 2.2	22.8 ± 2.1	28.5 ± 0.8	25.3 ± 1.2
	% Change	+11.1%	+8.8%	−10.7%	+1.4%	−3.0%	+10.1%	−4.2%
Overstory density trees, ha^{-1} (trees >25 cm dbh)	Year 0	186 ± 6.6	168 ± 10.5	204 ± 15.8	193 ± 14.3	128 ± 9.3	177 ± 6.4	175 ± 9.9
	Year 13	182 ± 7.3	159 ± 10.0	172 ± 15.0	176 ± 14.6	126 ± 13.3	171 ± 6.6	158 ± 9.1
	% Change	−1.9%	−5.3%	−15.7%	−8.8%	−1.4%	−3.5%	−9.6%
Midstory density trees, ha^{-1} (trees 10–25 cm DBH)	Year 0	189 ± 19.5	219 ± 16.0	195 ± 22.9	157 ± 13.9	195 ± 21	204 ± 12.7	182 ± 11.5
	Year 13	196 ± 23.4	214 ± 15.3	102 ± 25.8	120 ± 18.0	139 ± 15	205 ± 13.8	120 ± 11.6
	% Change	+3.8%	−2.0%	−47.5%	−23.7%	−28.8%	+0.7%	−34.0%
Large sapling density trees, ha^{-1} (stems 3–9.9 cm DBH)	Year 0	526 ± 85.0	508 ± 60.9	494 ± 55.5	651 ± 72.7	530 ± 60.8	517 ± 50.8	535 ± 39.6
	Year 13	576 ± 111	501 ± 26.0	82 ± 42.7	164 ± 44.1	139 ± 38.1	539 ± 56.3	130 ± 24.2
	%Change	+9.5%	−1.4%	−83.4%	−74.8%	−73.7%	+4.1%	−75.6%
Open sky (%)	Year 0	5.5 ± 0.7	4.7 ± 0.8	3.8 ± 0.3	3.3 ± 0.6	4.1 ± 0.6	5.1 ± 0.5	4.1 ± 0.3
	Year 13	5.7 ± 0.9	4.7 ± 0.3	10.4 ± 1.6	11.0 ± 1.1	8.5 ± 1.1	5.2 ± 0.5	9.9 ± 0.8
	% Change	+0.2%	+0.0%	+6.6%	+7.7%	+4.4%	+0.04%	+5.8%

Table 4
Mortality[a] of midstory (10–25 cm DBH) trees, from year 0 (1995) to year 13 (2008) on 18 unburned and 27 burned plots.

Species/taxa	Mean DBH (cm)	Trees, year 0 Unburned (n)	Trees, year 0 Burn (n)	Unburned mortality (%)	Burned mortality (%)	Burn – unburned mortality (%)
Acer rubrum	14.9	183	157	6.0	49.0	43.0
Oxydendrum arboretum	14.8	29	30	20.7	63.3	42.6
Quercus alba	18.5	85	107	45.9	66.7	20.8
Carya spp.	16.9	46	72	8.7	26.4	17.7
Liriodendron tulipifera	16.6	19	39	15.8	23.1	7.3
Nyssa sylvatica	13.7	35	44	2.9	9.1	6.2
Quercus prinus	19.0	24	48	12.5	14.6	2.1
Other shade-tolerant species[b]	13.6	28	78	25.0	33.4	8.4
Other intolerant species[c]	17.2	9	40	33.0	42.5	9.5
Total, all midstory trees	16.0	459	615	16.8	39.5	22.7

[a] Mortality is defined here as mortality of the original stem, regardless of whether it resprouted.
[b] Other shade-tolerant species (n, year 0): *Acer saccharum* (25), *Fagus grandifolia* (24), *Cornus florida* (20), *Ulmus rubra* (16), *Aesculus flava* (14), *Tilia americana* (5), *Amelanchier arborea* (1), *Cercis canadensis* (1).
[c] Other intolerant species (n, year 0): *Quercus rubra* (17) *Quercus velutina* (13), *Quercus coccinea* (12), *Fraxinus americana* (5), *Sassafras albidum* (2).

years 0 to 13, despite an 80% decrease in flowering dogwood density, the result of mortality attributed to dogwood anthracnose (*Discula destructiva* Redlin). The decrease in dogwood on unburned plots was balanced by a 90% increase in the density of American beech. In year 13, 88% and 98% of large saplings were shade-tolerant in burned and unburned units, respectively.

The reduced densities of midstory trees and large saplings on burned plots resulted in a modest but significant increase in canopy openness. By year 13, open sky was significantly greater ($F_{1,19.4} = 16.7$, $p < 0.001$) in burned plots (LS mean = 9.8 ± 1.1%) than in unburned plots (LS mean = 5.2 ± 1.1%) (Fig. 2e). Only 3 of 18 unburned plots had >6% open sky in year 13 (range = 2.9–11.6%); by contrast, 25 of 27 burned plots had >6% open sky (range = 4.8–18.6%).

3.2. Tree mortality

Mortality of midstory trees (10–25 cm DBH in year 0), defined here as the aboveground death of the original stem, regardless of whether repsrouting occurred, was 16.8% on unburned plots and 39.5% on burned plots, over 13 years (Table 4). Before fire treatments, red maple was the most abundant species in the midstory, accounting for 32% of trees; it also exhibited the largest difference in mortality between unburned (6.0%) and burned plots (49.0%). White oak was the second most abundant species in the midstory in year 0; although it had the greatest mortality on burned plots (63.3%), nearly one-half (45.9%) of midstory white oaks also died on unburned plots. For most other common species (yellow-poplar, blackgum, chestnut oak), and species groups (‘other shade-tolerant species’, ‘other intolerant species’) in the midstory stratum, differences in mortality between burned and unburned plots were <10%.

Mortality of larger overstory trees (>25 cm DBH) was 18.6% on burned plots and 10.8% on unburned plots, from year 0 to 13. In year 0, oaks and hickories constituted 87% of overstory trees in plots that would remain unburned and 88% of overstory trees in plots assigned to be burned. The great majority of overstory trees that had died over the 13-years were oaks and hickories, on both unburned (93.0%) and burned (94.5%) plots.

3.3. Small sapling dynamics

Prior to fire treatments, shade-tolerant species dominated the small sapling strata (stems 1.4 m tall to 2.9 cm DBH) on dry (IMI <45) and mesic (IMI >45) plots in all five units (Figs. 3 and 4a and d); Five species (red maple, blackgum, American beech, flowering dogwood, sugar maple) comprised 84% of the shade-tolerant stems. On dry plots ($n = 24$), 78% of small saplings were shade-tolerant and 12% were oak + hickory. On mesic plots ($n = 21$) 95% of small saplings were shade-tolerant and oak + hickory accounted for only 1% of stems.

By year 4, after two or four fires on burned plots, small sapling densities had been reduced by 98% and 92% on dry and mesic plots, respectively, as nearly all stems had been topkilled (Figs. 3b and d and 4b and e). Most topkilled stems resprouted (T. Hutchinson, personal observation) but remained <140 cm tall and thus were not tallied.

By year 13, 3 or 4 years after the last fire, the small sapling layer had redeveloped on the dry burned plots but not on the mesic burned plots (Figs. 3b,d and 4c,f). Among the burned plots ($n = 27$), there were significantly more small saplings ($F_{1,18} = 15.6$, $p < 0.001$) on dry plots (LS mean = 1472 ± 365 stems ha^{-1}) than on mesic plots (LS mean = 263 ± 93 stems ha^{-1}) in year 13. Shade-tolerant species were less dominant by year 13; the relative density of oak + hickory was significantly greater ($F_{1,9.8} = 13.0$, $p = 0.005$) on burned plots (LS mean = 0.431 ± 0.06) than on unburned plots (LS mean = 0.133 ± 0.07).

In year 13, multi-stemmed stump sprouts >140 cm tall (originating from topkilled stems >5 cm basal diameter) occurred at very low densities. On burned plots, the mean density of stump sprouts was 49 stems ha^{-1} (mean 2.5 stems per individual rootstock); the majority of stump sprouts were sourwood (*Oxydendrum arboretum* (L.) DC.) and red maple. Unburned plots had a mean of 9 stump sprouts per ha (mean 3.0 stems per individual rootstock) in year 13.

3.4. Advance regeneration

ANCOVA indicated that the total density of advance regeneration (stems 30 cm tall to 2.9 cm DBH) in year 13 was significantly greater ($F_{1,19.7} = 10.3$, $p = 0.005$) on burned plots (LS mean = 8584 ± 1756 stems ha^{-1}) than on unburned plots (LS mean = 4672 ± 1006 stems ha^{-1}) (Fig. 5d). The greater stem densities found on burned plots were largely a function of those plots having more oak + hickory and sassafras.

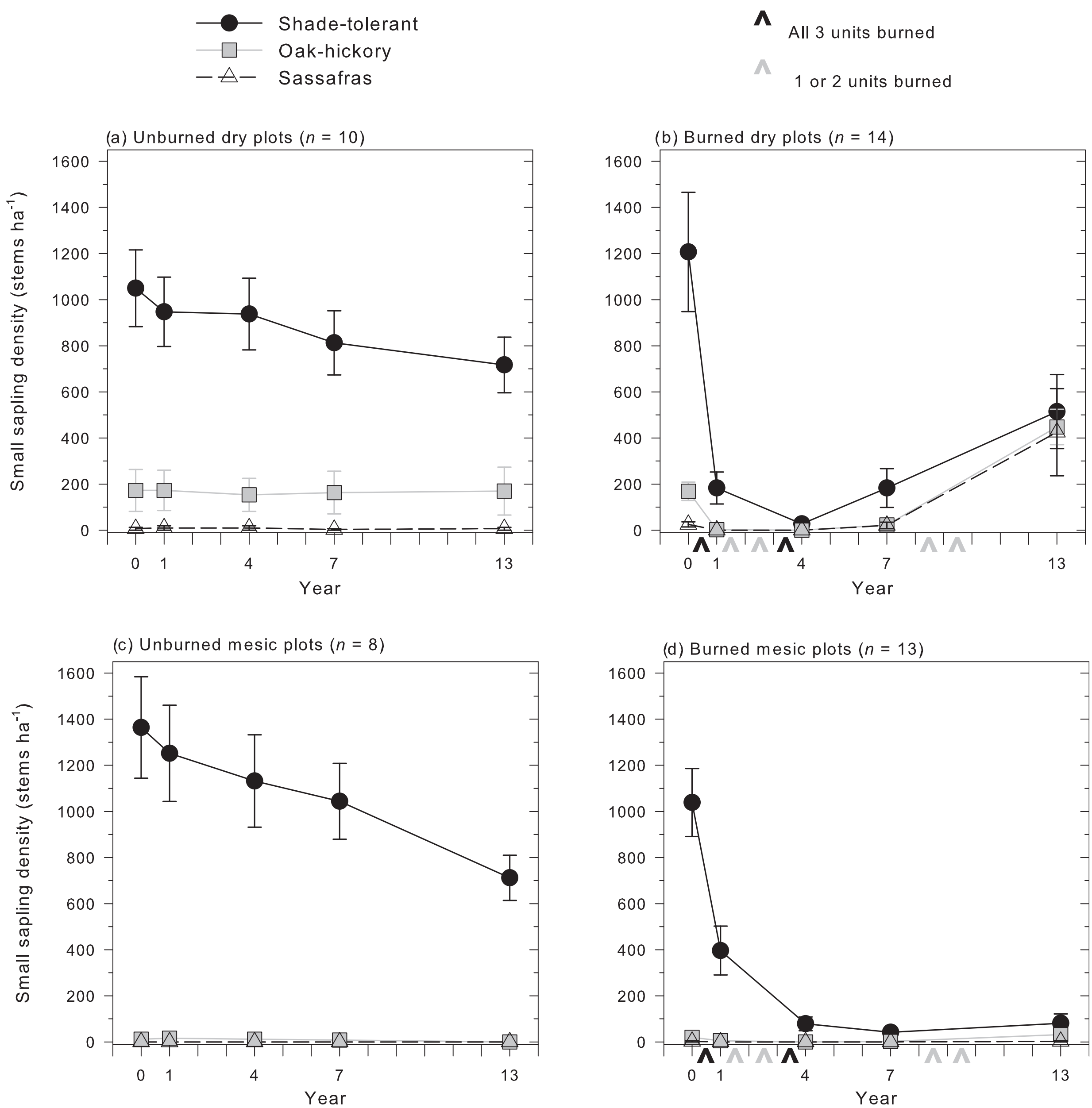

Fig. 3. Density (mean ± S.E.) of small saplings (1.4 m tall to 2.9 cm DBH) on (a) unburned dry plots, (b) burned dry plots, (c) unburned mesic plots, and (d) burned mesic plots in years 0 (pre-burn), 1, 4, 7, and 13, for the three major species groups.

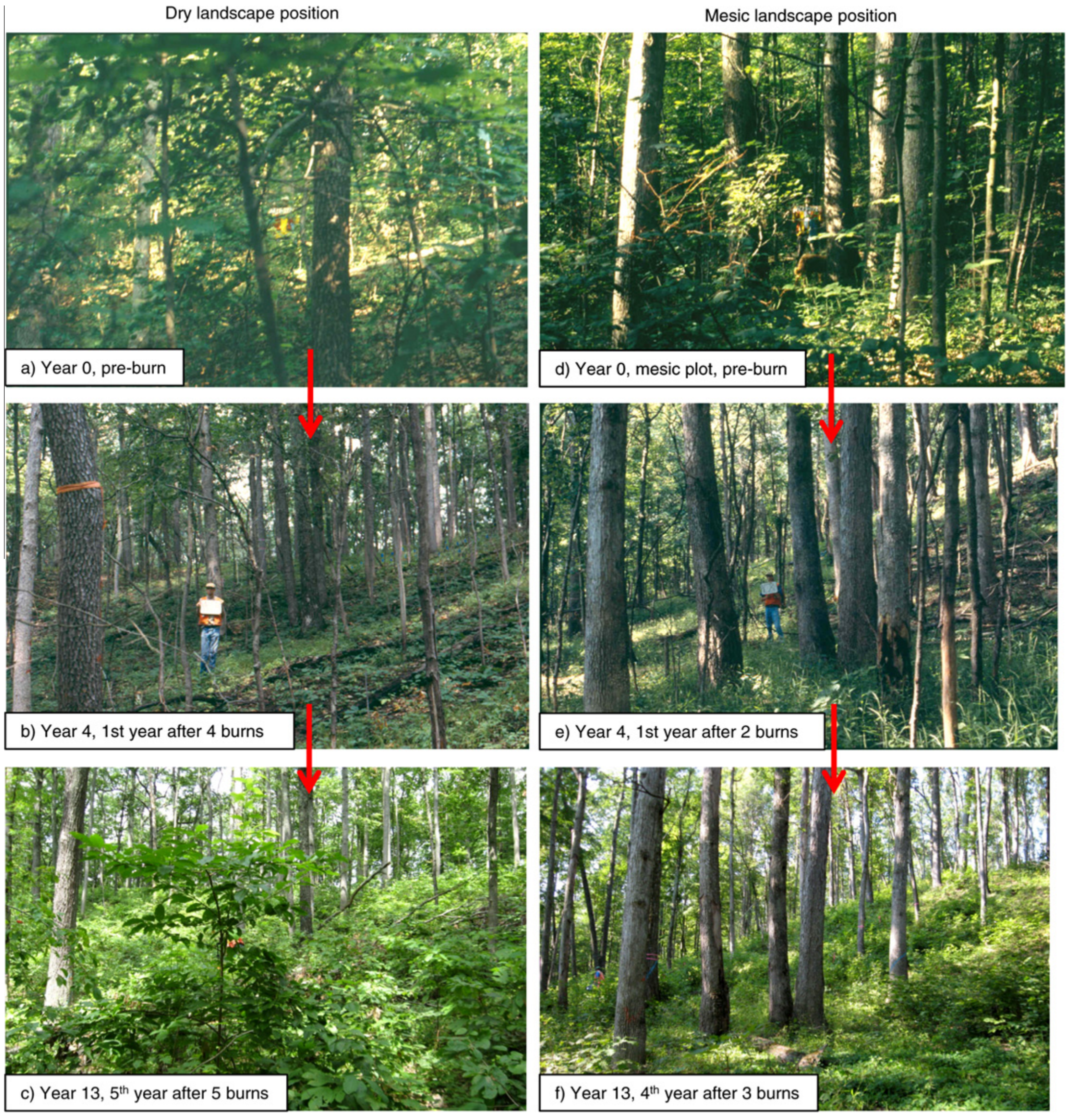

Fig. 4. Repeated photographs of two burned plots (one dry, one mesic) showing understory structure in years 0 (pre-burn), 4, and 13.

The density of oak + hickory advance regeneration was significantly greater ($F_{1,41.3} = 11.0$, $p = 0.002$) on burned plots (LS mean = 3586 ± 1286 stems ha^{-1}) than on unburned plots (LS mean = 1380 ± 519 stems ha^{-1}) (Fig. 5a). Regression analysis illustrates the relationships of the weighted frequency of oak + hickory seedlings in year 0, a surrogate measure of density and size before treatments, to the density of oak + hickory advance regeneration in year 13, for both burned and unburned plots (Fig. 6). For oak + hickory seedlings ⩾30 cm tall, more than one-half of burned plots (n = 17 of 27) had ⩾3000 per ha compared to only 2 of 18 unburned plots. Within the oak + hickory group, the most abundant species were white oak, hickories, and black oak (Table 5); the mean density (±std. error) of white oak ⩾30 cm tall was more than 5X greater on burned plots (1529 ± 374 stems ha^{-1}) than on unburned plots (283 ± 185 stems ha^{-1}) in year 13.

The density of sassafras (⩾30 cm tall) was highly variable in year 13, ranging from zero on one-third of plots to more than 7000 stems ha^{-1} on several plots. On plots where sassafras was present (n = 27) the density of advance regeneration was significantly greater ($F_{1,12.6} = 35.5$, $p < 0.001$) on burned plots (LS mean = 2136 ± 618 stems ha^{-1}) than on unburned plots (306 ± 110 stems ha^{-1}) (Fig. 5c).

In contrast to oak + hickory and sassafras, the density of shade-tolerant species was not significantly different ($F_{1,18.3} = 0.82$, $p = 0.378$) on burned (LS mean = 2882 ± 863 stems ha^{-1}) and unburned (LS mean = 2335 ± 718 stems ha^{-1}) plots in year 13 (Fig. 5d). Red maple was the most abundant shade-tolerant species and its mean density was more than 2X greater on burned plots (1285 ± 384 stems ha^{-1}) than on unburned plots (504 ± 183 stems ha^{-1}) in year 13 (Table 5). Among the other most common shade-tolerant species, blackgum and sourwood had higher densities on burned plots than on unburned plots, while white ash (*Fraxinus Americana* L.), American beech, and common serviceberry (*Amelanchier arborea* [Michx. f.] Fernald) densities were higher on unburned plots than on burned plots.

The 'other species' group, shade-intolerant species other than oaks, hickories, and sassafras, occurred at low densities overall. American chestnut (*Castanea dentata* (Marshall) Borkh.) and yellow-poplar were the two most abundant species in this group (Appendix).

The relative density of oak + hickory was significantly greater ($F_{1,42} = 5.0$, $p = 0.030$) on burned plots (LS mean = 0.441 ± 0.032) than on unburned plots (LS mean = 0.319 ± 0.040) (Fig. 5e). On burned plots where oak + hickory was abundant, several compet-

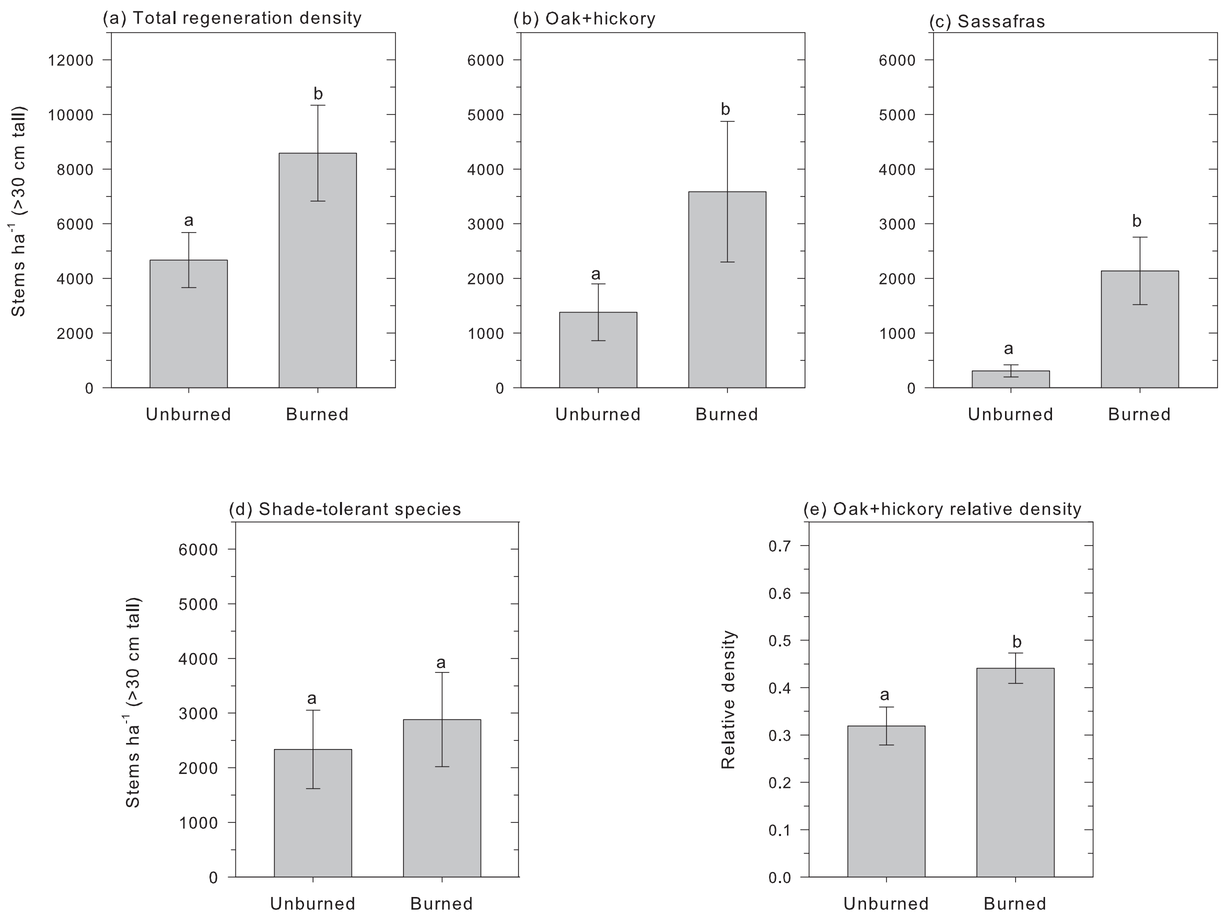

Fig. 5. Results of ANCOVA for density of advance regeneration (stems 30 cm tall to 2.9 cm DBH) in year 13: (a) total regeneration, (b) oak + hickory, (c) sassafras, (d) shade-tolerant species, (e) relative density of oak + hickory. Bars represent adjusted LS means (±S.E.). Different letters above the bars indicate significant differences between burned and unburned plots.

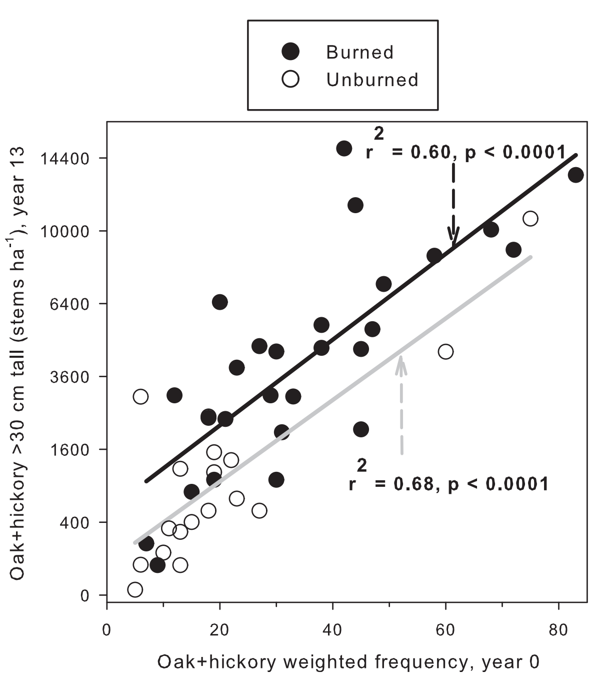

Fig. 6. Simple linear regression analysis showing the relationship between oak + hickory weighted frequency in year 0 (independent variable) and density of oak + hickory advance regeneration (stems 30 cm tall to 2.9 cm DBH) in year 13, for unburned (n = 18) and burned (n = 27) plots.

ing species also had high densities. Oak + hickory density on burned plots was positively correlated with the density of red maple (r = 0.75, p < 0.001), sassafras (r = 0.52, p = 0.006), blackgum (r = 0.46, p = 0.017), sourwood (r = 0.42, p = 0.029), and flowering dogwood (r = 0.41, p < 0.033).

Simple linear regression analysis of all plots showed that the density of oak + hickory advance regeneration (stems ⩾30 cm tall) in year 13 was strongly related to several predictor variables (Fig. 7). Regardless of fire treatment, the weighted frequency of oak + hickory regeneration in year 0 was the strongest predictor of oak + hickory density in year 13 (r^2 = 0.67). Oak + hickory density was also significantly related to three measures of stand structure: it was inversely related to large sapling density (r^2 = 0.44, p < 0.0001) and stand density (r^2 = 0.33, p < 0.0001) and it was positively related to % open sky (r^2 = 0.31, p < 0.0001). Together, these three regressions show that, in general, there was more oak + hickory advance regeneration in the more open-structured plots, which were plots that had been burned. Oak + hickory density was also inversely, but rather weakly, related to the IMI (r^2 = 0.15, p = 0.008); the greatest densities of oak + hickory occurred on relatively dry plots, those with IMI <50.

4. Discussion

Repeated prescribed fires altered stand structure by greatly reducing the density of saplings and also by moderate reductions in the density of midstory trees. Fire had little effect on the density of overstory trees (>25 cm DBH). Only a few studies have docu-

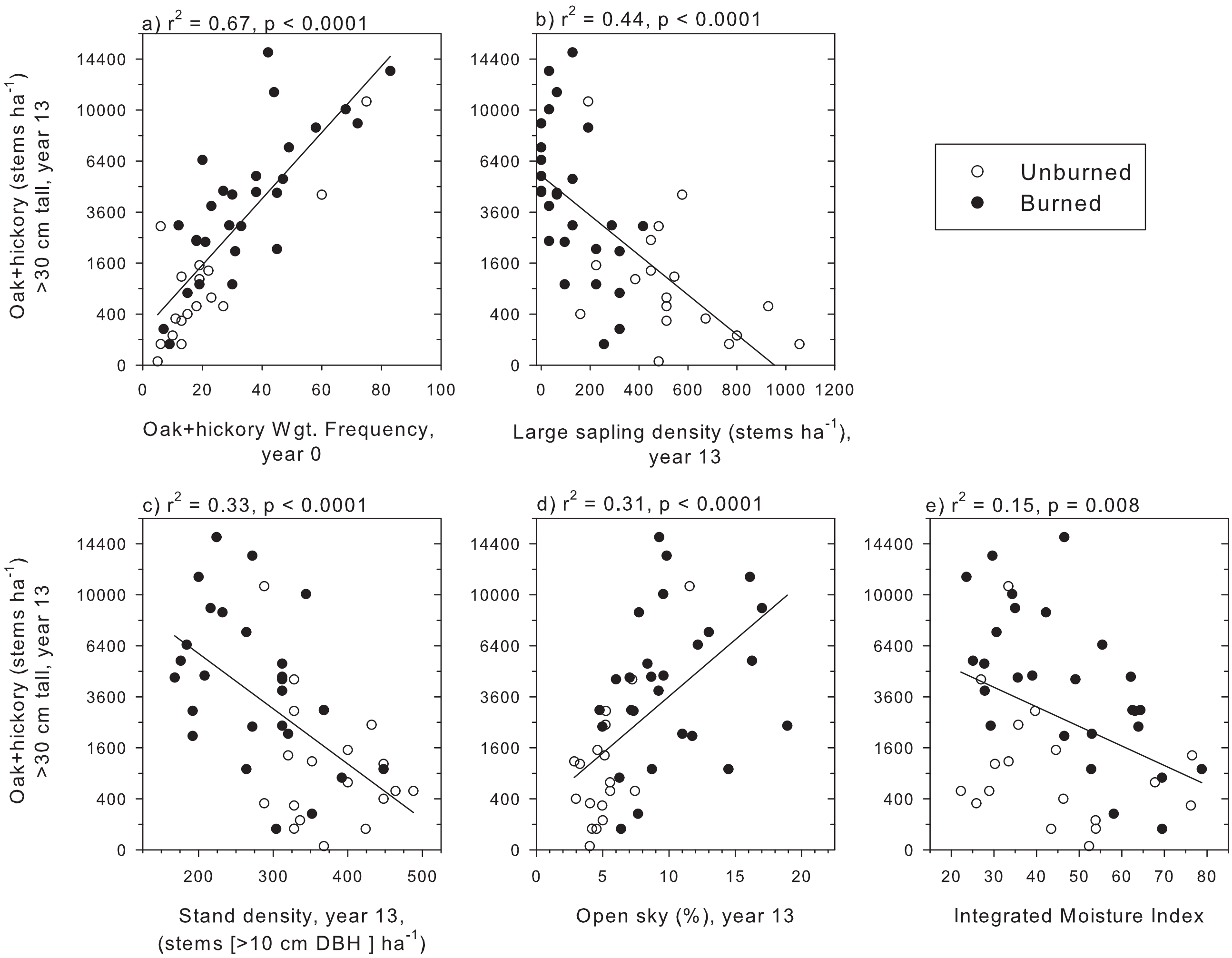

Fig. 7. Simple linear regression analysis of the relationship between the density of oak + hickory advance regeneration (stems 30 cm tall to 2.9 cm DBH) (dependent variable) and five independent variables, for unburned ($n = 18$) and burned ($n = 27$) plots collectively.

mented the longer-term effects of repeated burns on the structure of oak forests. On ridgetop sites in Kentucky, Blankenship and Arthur (2006) reported effects similar to ours: over a period of 9 years, after two or three prescribed fires, burned sites exhibited a 30% reduction in the density of trees >10 cm DBH and a 91% reduction in the density of saplings 2–10 cm DBH. In less productive, lower BA (~16 $m^2\ ha^{-1}$) stands in the Missouri Ozarks, 4–10 prescribed fires in a 10-year period resulted in only minor reductions (<4%) in the density of trees >11 cm DBH, while the density of saplings 4–11 cm DBH was reduced by only 50% (Dey and Fan, 2009). The Ozark sites likely exhibited less topkill because thin-barked fire-sensitive species (e.g., red maple, American beech, sourwood) were much less common than in the Ohio and Kentucky sites. In Pennsylvania, mixed-oak stands that had been burned 3 or 4 times during military exercises exhibited BA of 20–24 $m^2\ ha^{-1}$, compared to adjacent unburned stands with BA of 30–32 m^2/ha (Signell et al., 2005). One or more of these unplanned wildfires may have been more intense than typical prescribed fires and thus resulted in greater mortality of overstory trees.

Red maple was the most abundant species in the midstory at the beginning of our study and it also exhibited the greatest level of midstory mortality (death of original stem) on burned plots, as compared to very low rates of mortality on unburned plots. The susceptibility of the thin-barked red maple to fire-induced topkill has been shown in other studies (Hare, 1965; Harmon, 1984; Bova and Dickinson, 2005). White oak, the second most abundant species in the midstory, exhibited substantial mortality on both burned and unburned plots, a finding also reported by Blankenship and Arthur (2006). Mortality of white oak, which is intolerant of heavy shade, is likely the result of self-thinning of suppressed and intermediate trees during stand development (Oliver and Larson, 1996). Among other common species in the midstory, chestnut oak, blackgum, and yellow-poplar exhibited the lowest levels of mortality on burned plots, as compared to mortality in unburned plots; all three species have relatively thick bark when DBH is >10 cm and have been shown to be resistant to fire-caused mortality (Starker, 1934; Maslen, 1989; Regelbrugge and Smith, 1994; Bova and Dickinson, 2005). This variability in midstory mortality among species indicates that the ability of prescribed fire to reduce stand density is partially dependent on species composition. In our study, the AR 3X unit had the greatest relative density of red maple (42%) in the midstory and also exhibited the greatest reduction in midstory density (48%). However, fire intensity was likely greater on the AR 3X unit, because overstory density was also reduced to a greater extent on that unit. During the first five years of the study, when the two 5X units were burned annually (years 1–4), the annual consumption of leaf litter reduced fire intensity on those units (Hutchinson et al., 2005b). Our results suggest that annual burning, which limits fire intensity, also reduces the capacity of fire to alter stand structure.

The density and species composition of the small sapling layer (stems 1.4 m tall to 2.9 cm DBH) was dynamic over time on dry

Table A1
Mean density (S.E.) of advance regeneration (stems 30 cm tall to 2.9 cm DBH) by species in year 13 on unburned plots ($n = 18$) and plots burned 3–5 times ($n = 27$).

Species	Common name	Species group	Mean density (stems ha^{-1}), year 13	
			Unburned plots	Burned plots
Carya spp.	Hickories	Oak + hickory	494 (156)	973 (142)
Quercus alba	White oak	Oak + hickory	283 (185)	1529 (374)
Quercus coccinea	Scarlet oak	Oak + hickory	207 (634)	571 (213)
Quercus prinus	Chestnut oak	Oak + hickory	266 (150)	656 (232)
Quercus rubra	Northern red oak	Oak + hickory	46 (14)	231 (62)
Quercus velutina	Black oak	Oak + hickory	303 (170)	1018 (200)
Sassafras albidum	Sassafras	Sassafras	200 (101)	2406 (594)
Acer rubrum	Red maple	Shade-tolerant	504 (183)	1285 (384)
Acer saccharum	Sugar maple	Shade-tolerant	136 (78)	10 (5)
Amelanchier arborea	Common serviceberry	Shade-tolerant	301 (115)	160 (46)
Carpinus caroliniana	Musclewood	Shade-tolerant	170 (79)	185 (143)
Cercis canadensis	Eastern redbud	Shade-tolerant	–	306 (189)
Cornus florida	Flowering dogwood	Shade-tolerant	39 (19)	285 (59)
Fagus grandifolia	American beech	Shade-tolerant	367 (75)	127 (28)
Fraxinus americana	White ash	Shade-tolerant	412 (96)	162 (45)
Nyssa sylvatica	Blackgum	Shade-tolerant	388 (72)	545 (121)
Oxydendrum arboretum	Sourwood	Shade-tolerant	184 (54)	238 (91)
Castanea dentata	American chestnut	Other species	57 (32)	145 (35)
Liriodendron tulipifera	Yellow-poplar	Other species	28 (12)	97 (46)
Minor species[a]		Mixed	182 (54)	116 (31)
Total, all species			4566 (717)	11044 (1560)

[a] Minor species: *Aesculus flava* (Yellow buckeye), *Asimina triloba* (pawpaw), *Crataegus* spp. (hawthorn), *Diospyros virginiana* (common persimmon), *Juglans nigra* (black walnut), *Ostrya virginiana* (Eastern hophornbeam), *Prunus serotina* (black cherry), *Quercus stellata* (post oak), *Tilia americana* (American basswood), *Ulmus rubra* (slippery elm), *Viburnum prunifolium* (blackhaw).

plots that were burned. After virtually all small saplings had been topkilled by year 4, the small sapling layer had redeveloped on the dry burn plots 4–5 years after the last fire and the species composition had shifted to have more saplings of oak + hickory and sassafras and fewer of shade-tolerant species. The significant increase in the relative density of small oak + hickory saplings from year 0 to year 13 has rarely if ever been reported after prescribed fires without additional treatments. Signell et al. (2005) reported that oak saplings (stems >1.45 m tall to 7.6 cm DBH) had developed in younger stands (50–60 years since origination) in Pennsylvania that had been burned repeatedly by wildfires.

In contrast to the dry burn plots, the small sapling layer on mesic burn plots had not redeveloped by year 13, even though stand density and canopy openness were similar on dry and mesic plots. We hypothesize that several factors may have contributed to this phenomenon. First, despite similar stand structure on dry and mesic burned plots, solar radiation to the understory layer was likely greater on the dry plots due to their southern aspect. In addition, trees allocate a greater proportion of primary production to root growth on xeric sites than on mesic sites (Comeau and Kimmins, 1989). On the Arch Rock site in our study, Dress and Boerner (2001) showed that fine root biomass and production were greater on dry sites than on mesic sites. The greater allocation to roots on dry sites may have facilitated more vigorous resprouting after topkill from belowground carbohydrate reserves, from oaks and other species as well. Sprouting vigor also may have been limited more on mesic sites due to competition from perennial forbs and ferns, which are typically more abundant than on dry sites.

In year 13, stump sprouts >1.4 m tall that originated from large saplings or trees occurred at low densities on burned plots. This finding suggests that the great majority of small saplings that were present in year 13 originated from seedlings or small saplings (rather than large sapling and trees) present at the beginning of the study. Although we recorded only stump sprouts that were >1.4 m tall, it is clear that sprouting, particularly that of red maple, was less vigorous in our study than after repeated burns on dry Kentucky ridgetops (Blankenship and Arthur, 2006). In the Kentucky study, there were up to 6000 red maple sprouts (>50 cm tall) per ha 2 years after the last of three prescribed fires (Blankenship and Arthur. 2006). Fire behavior and seasonality were similar in the two studies. However, prior to burning, red maple was more abundant in the Kentucky sites than in our Ohio sites: red maple trees (>10 cm DBH) were about 2X more abundant and saplings (2–10 cm DBH) were about 4X more abundant. The greater size and abundance of red maple on the Kentucky sites likely contributed to more abundant post-fire sprouting. The larger number of fires in our study (three or five burns) than on the Kentucky sites (two or three burns) may have reduced sprouting vigor. In our study, topkilled saplings and poles were forced to resprout up to five times under low-light conditions. Repeated topkilling may have depleted belowground carbohydrate reserves, particularly for species with lower root:shoot ratios. In addition, each topkill/resprout event produced new sprouts close to the forest floor and thus available for browsing by white-tailed deer (*Odocoileus virginianus* Zimmermann), which occur at moderate densities of approximately 6/km^2 (post-hunting season) in Vinton County (Apsley and McCarthy, 2004).

In this study, our ability to quantify the effects of repeated fires on advance regeneration (seedlings >30 cm tall) is limited by several factors. First, the initial plot design for sampling tree regeneration was inadequate to capture the abundance of seedlings >30 cm tall. However, we used seedling frequency data to create a pre-treatment "weighted frequency" (weighted by size class) that served as a surrogate for pre-treatment density. The weighted frequency was strongly correlated with the density of advance regeneration in year 13, on both control and burned plots, particularly for oak + hickory and sassafras. A second limitation is that survival and growth of individual seedlings, saplings, and sprouts were not followed over time; that information can provide a more detailed and mechanistic understanding of fire effects over time (e.g., see Brose and Van Lear, 1998; Alexander et al., 2008; Fan et al., 2012). Third, our study does not provide information on how fire affected regeneration from seed. For the oaks, quantifying the establishment, survival, and growth of seedlings from periodic acorn crops is important to understanding the regeneration process in response to silvicultural treatments. Despite these limitations, our study does provide a "snapshot" of advance regeneration density on unburned and burned plots after 13 years of periodic fires, across a range of topographic and stand structural conditions.

Among the common species/groups in the advance regeneration layer, oak + hickory and sassafras were more abundant on burned plots than on unburned plots in year 13, after adjustment for pre-treatment frequency. When the study began, saplings of oak + hickory and sassafras occurred at very low densities, suggesting that the advance regeneration (stems >30 tall) of these species on burned plots in year 13 consisted primarily of sprouts from seedlings (rather than saplings) that were present in year 0. This assumption is reinforced by the strong correlation of oak + hickory and sassafras advance regeneration in year 13 with the weighted seedling frequency of these species in year 0. For the oaks and hickories, however, we do not know what proportion of advance regeneration in year 13 was from new seedlings that established during the course of the study. If we assume that the majority of the oak advance regeneration in year 13 was already established before burning started, then the positive effects of fire were to promote the development of larger seedlings on sites that are "intrinsic" or "ambivalent" accumulators of oak regeneration (sensu Johnson et al., 2009) rather than by facilitating the establishment of new seedlings on higher-quality sites that are "recalcitrant" accumulators of oak seedlings. Greater sassafras densities on burned plots likely resulted from expansion via root suckering from established seedlings (Burns and Honkala, 1990). Other studies have also shown an increase in the density and size of sassafras regeneration after prescribed fire (Blankenship and Arthur, 2006; Alexander et al., 2008).

In contrast to oak + hickory and sassafras, we found that the density of shade-tolerant species was not significantly different on burned and unburned plots in year 13. In year 0, shade-tolerant species were abundant in the sapling layer and large seedlings (>30 cm tall) occurred frequently. Thus, on burned plots, the advance regeneration of shade-tolerant species in year 13 likely originated from sprouts of both saplings and seedlings that were present in year 0. Unlike the oak + hickory species group, in which the mean density of all six taxa was greater on burned plots than on unburned plots in year 13, about half of the shade-tolerant species had higher densities on burned plots and about half of the species had higher densities on unburned plots (Table 5). Although we analyzed the shade-tolerant species as a group, our results suggest that several species (e.g., red maple, blackgum, flowering dogwood) were more capable of sprouting repeatedly after topkill than were others (e.g., white ash, American beech, serviceberry, sugar maple).

Even though multiple fires caused large decreases in the density of understory stems, reductions in basal area and canopy cover were much less than is considered optimal for the development of small oak seedlings into larger and more competitive regeneration (Loftis, 1990; Crow, 1992; Johnson et al., 2009; Brose, 2008). Gottschalk (1985) showed that northern red oak (*Quercus rubra* L.) and black oak seedlings required more than 20% of full sunlight to exhibit maximal diameter growth, which is equivalent to a 40% basal area reduction in a mature stand; in our study, basal area in burned stands was reduced by a mean of only 4.2%. Among the five common oaks in our study, seedlings of white oak are the slowest growing, most shade-tolerant, and least responsive to increasing light levels (Rebbeck et al., 2011). White oak was the most abundant oak on the burned plots in year 13. While the light environment created by repeated burns was not sufficient for rapid growth of seedlings, it may have been sufficient for increased survival and modest growth of the more shade-tolerant white oak.

5. Conclusions and management implications

In mature forests, research has shown that a single low-intensity prescribed fire has very little effect on stand structure and the composition and abundance of tree regeneration (see Brose et al., 2006). In this study, multiple low-intensity fires forced saplings, which were predominantly shade-tolerant species, to resprout repeatedly under low-light conditions, thus limiting their sprouting vigor. Further reduction in sprouting vigor and increased mortality of non-oak seedlings and saplings may be achieved by prescribed fires conducted during the growing season (Brose and Van Lear, 1998). The sprouting capacity of oak seedlings following growing-season burns has been shown to be greater than competitors due to oak's greater biomass allocation to roots; however, small oak seedlings (root collar diameter <0.65 cm) are susceptible to significant mortality in growing-season burns (Brose and Van Lear, 2004).

Overall, the results of this study are mixed with respect to the effects of repeated fires on the competitive status of oak + hickory regeneration. Repeated burns on dry plots reduced the dominance of shade-tolerant species in the small sapling layer, and resulted in the development of oak + hickory and sassafras saplings. However, small saplings of oak + hickory did not develop on mesic plots that were burned repeatedly. Presumably, oak + hickory seedlings on dry plots had greater root biomass at the beginning of the study, which facilitated sprouting after fire and the development of larger seedlings and saplings by year 13. Though the density of oak + hickory advance regeneration was greater on burned plots than on unburned plots in year 13, sassafras and several shade-tolerant species, including red maple, were also more abundant on burned plots than on unburned plots.

Fire alone did not reduce stand density enough to facilitate rapid growth of oak seedlings. In order to favor the development of larger oak and hickory seedlings, repeated burns should be coupled with other techniques to reduce stand density. A companion study on these same sites showed that the formation of moderate-sized (200–400 m^2) canopy gaps after multiple burns (but not caused by the burns) led to the development of much greater densities of larger oak + hickory seedlings (Hutchinson et al., 2012). Gaps in the three burned stands had a mean density of 6911 larger (>60 cm tall) oak + hickory seedlings per ha, compared to the plots in this study (2702 stems ha^{-1}), in which gaps were largely absent. Together, this study and the gap study show that although the competitive position of oak + hickory regeneration may remain unclear in closed-canopy stands that have been burned, the formation of canopy gaps after repeated burns can lead to more rapid height growth of oak + hickory seedlings in a higher light environment. To further reduce stand density without harvesting overstory trees, repeated fires, which effectively reduce the density of stems <15 cm DBH, could be coupled with herbicide treatment (stem injection) of undesirable midstory trees that are too large to be topkilled by fire.

Prior to the initiation of prescribed fire treatments in these stands, oak + hickory seedlings were present at moderately high densities but were small in stature. If oak + hickory seedlings are sparse prior to initiating a burning regime, then repeated burns are not likely to improve the competitive status of oak + hickory seedlings unless establishment from seed is enhanced.

Acknowledgments

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Appendix A

See Table A1.

References

Abrams, M.D., 1992. Fire and the development of oak forests. Bioscience 42, 346–353.

Abrams, M.D., 1998. The red maple paradox-what explains the widespread expansion of red maple in eastern forest? Bioscience 48, 355–364.

Abrams, M.D., 2003. Where has all the white oak gone? Bioscience 53, 927–939.

Abrams, M.D., Nowacki, G.J., 1992. Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania. Bull. Torrey Bot. Club 119, 19–28.

Alexander, H.D., Arthur, M.A., Loftis, D.L., Green, S.R., 2008. Survival and growth of upland oak and co-occurring competitor seedlings following single and repeated prescribed fires. For. Ecol. Manage. 256, 1021–1030.

Apsley, D.K., McCarthy, B.C., 2004. White-tailed deer herbivory on forest regeneration following fire and thinning treatments in southern Ohio. In: Yaussy, D.A., Hix, D.M., Long, R.P., Goebel, P.C., (Eds.), Proceedings, 14th Central Hardwood Forest Conference. Gen. Tech. Rep. NE-316, USDA Forest Service, Northeastern Research Station, Newtown Square, PA, pp. 461–471.

Barnes, T.A., Van Lear, D.H., 1998. Prescribed fire effects on advanced regeneration in mixed hardwood stands. Southern J. Appl. Forest. 22, 138–142.

Beatley, J.C., Bartley, F., 1959. The primeval forests of a periglacial area in the Allegheny Plateau (Vinton and Jackson Counties, Ohio). Bull. Ohio Biol. Surv. 1, 1–166.

Blankenship, B.A., Arthur, M.A., 2006. Stand structure over 9 years in burned and fire-excluded oak stands on the Cumberland Plateau, Kentucky. For. Ecol. Manage. 225, 134–145.

Boerner, R.E.J., Sutherland, E.K., 2003. Physiography, geology, and soil classification. In: Sutherland, E.K., Hutchinson, T.F. (Eds.), Characteristics of mixed-oak Forests in Southern Ohio Prior to the Reintroduction of Fire. Gen. Tech. Rep. NE-299. USDA Forest Service, Northeastern Research Station, Newtown Square, PA, pp. 43–45.

Boerner, R.E.J., Brinkman, J.A., Sutherland, E.K., 2004. Effects of fire at two frequencies on nitrogen transformations and soil chemistry in a nitrogen-enriched forest landscape. Can. J. For. Res. 34, 609–618.

Bova, A.S., Dickinson, M.B., 2005. Linking surface-fire behavior, stem heating, and tissue necrosis. Can. J. For. Res. 35, 814–822.

Brose, P.H., 2008. Root development of acorn-origin oak seedlings in shelterwood stands on the Appalachian Plateau of northern Pennsylvania, 4-year results. For. Ecol. Manage. 255, 3374–3381.

Brose, P.H., Van Lear, D.H., 1998. Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. Can. J. For. Res. 28, 331–339.

Brose, P.H., Van Lear, D.H., 2004. Survival of hardwood regeneration during prescribed fires: the importance of root development and root collar location. In: Spetich, M.A., (Ed.), Upland Oak Ecology Symposium: History, Current Conditions, and Sustainability. Gen. Tech. Rep. SRS-73. USDA Forest Service, Southern Research Station, Asheville, NC, pp. 123–127.

Brose, P.H., Schuler, T.M., Ward, J.S., 2006. Responses of oak and other hardwood regeneration to prescribed fire, what we know as of 2005. In: Dickinson, M.B., (Ed.), Fire in Eastern Oak Forests: Delivering Science to Land Managers. Gen. Tech. Rep. NRS-P-1. USDA Forest Service, Northern Research Station, Newtown Square, PA, pp. 123–135.

Brose, P.H., Gottschalk, K.W., Horsley, S.B., Knopp, P.D., Kochenderfer, J.N., McGuinness, B.J., Miller, G.W., Ristau, T.E., Stoleson, S.H., Stout, S.L., 2008. Prescribing Regeneration Treatments for Mixed-oak Forests in the mid-Atlantic Region. Gen. Tech. Rep. NRS-33. USDA Forest Service, Northern Research Station, Newtown Square, PA, pp. 90.

Burns, R.M., Honkala, B.H., 1990. Silvics of North America. vol. 2. Hardwoods. For. Serv. Agric. Handb. 654, USDA, Washington, DC.

Carmean, W.H., 1965. Black oak site quality in relation to soil and topography in southeastern Ohio. Soil Sci. Soc. Amer. Proc. 29, 308–312.

Comeau, P.G., Kimmins, J.P., 1989. Above- and below-ground biomass and producition of lodgepole pine on sites with differing soil moisture regimes. Can. J. For. Res. 19, 447–454.

Crow, T.R., 1988. Reproductive mode and mechanisms for self-replacement of Northern Red Oak (*Quercus rubra*) – a review. For. Sci. 34, 19–40.

Crow, T.R., 1992. Population dynamics and growth patterns for a cohort of northern red oak (*Quercus rubra)* seedlings. Oecologia 91, 192–200.

Delcourt, P.A., Delcourt, H.R., Ison, C.R., Sharp, W.E., Gremillion, K.J., 1998. Prehistoric human use of fire, the eastern agricultural complex, and Appalachian oak-chestnut forests, paleoecology of Cliff Palace Pond, Kentucky. Am. Antiquity 63, 263–278.

Dey, D.C., Fan, Z., 2009. A review of fire and oak regeneration and overstory recruitment. In: Hutchinson, T.F., (Ed.), Proceedings of the 3rd Fire in Eastern Oak Forests Conference. Gen. Tech. Rep. NRS-P-46. USDA Forest Service, Northern Research Station, Newtown Square, PA, pp. 2–20.

Dress, W.J., Boerner, R.E.J., 2001. Root dynamics of southern Ohio oak-hickory forests, influences of prescribed fire and landscape position. Can. J. For. Res. 31, 644–653.

Dyer, J.M., 2001. Using witness trees to assess forest change in southeastern Ohio. Can. J. For. Res. 31, 1708–1718.

Fan, Z., Ma, Z., Dey, D.C., Roberts, S.D., 2012. Response of advance reproduction of oaks and associated species to repeated prescribed fires in upland oak-hickory forests. For. Ecol. Manage. 266, 160–169.

Fei, S., Steiner, K.C., 2007. Evidence for increasing red maple abundance in the Eastern United States. For. Sci. 53, 473–477.

Fesenmyer, K.A., Christensen, N.L., 2010. Reconstructing Holocene fire history in a southern Appalachian forest using soil charcoal. Ecology 91, 662–670.

Gottschalk, K.W., 1985. Effects of shading on growth and development of northern red oak, black oak, black cherry and red maple seedlings. I. Height, diameter, and root/shoot ratio. In: Dawson, J.O., Majerus, K.A., (Eds.), Proceedings of the Fifth Central Hardwood Forest Conference. SAF Publication 85–05. Society of American Foresters, Washington, DC, pp. 189–195.

Guyette, R.P., Muzika, R.M., Dey, D.C., 2002. Dynamics of an anthropogenic fire regime. Ecosystems 5, 472–486.

Hare, R.C., 1965. Contribution of bark to fire resistance. J. For. 63, 248–251.

Harmon, M.E., 1984. Survival of trees after low-intensity surface fires in Great Smoky Mountains National Park. Ecology 65, 796–802.

Hengst, G.E., Dawson, J.O., 1994. Bark properties and fire resistance of selected tree species from the central hardwood region of North America. Can. J. For. Res. 24, 688–696.

Hutchinson, T.F., Boerner, R.E.J., Sutherland, S., Sutherland, E.K., Ortt, M., Iverson, L.R., 2005a. Prescribed fire effects on the herbaceous layer of mixed-oak forests. Can. J. For. Res. 35, 877–890.

Hutchinson, T.F., Sutherland, E.K., Yaussy, D.A., 2005b. Effects of repeated fires on the structure, composition, and regeneration of mixed-oak forests in Ohio. For. Ecol. Manage. 218, 210–228.

Hutchinson, T.F., Long, R.P., Ford, R.D., Sutherland, E.K., 2008. Fire history and the establishment of oaks and maples in second-growth forests. Can. J. For. Res. 38, 391–403.

Hutchinson, T.F., Long, R.P., Rebbeck, J., Sutherland, E.K., Yaussy, D.A., 2012. Repeated prescribed fires alter gap-phase regeneration in mixed-oak forests. Can. J. For. Res. 42, 303–314.

Iverson, L.R., Prasad, A., 2003. A GIS-derived integrated moisture index. In: Sutherland, E.K., Hutchinson, T.F. (Eds.), Characteristics of Mixed-oak Forest Ecosystems in Southern Ohio Prior to the Reintroduction of Fire. Gen. Tech. Rep. NE-299. USDA Forest Service, Northeastern Research Station, Newtown Square, PA, pp. 29–41.

Iverson, L.R., Dale, M.E., Scott, C.T., Prasad, A., 1997. A GIS-derived integrated moisture index to predict forest composition and productivity of Ohio forests (USA). Landscape Ecol. 12, 331–348.

Jenkins, M.A., Parker, G.R., 1998. Composition and diversity of woody vegetation in silvicultural openings of southern Indiana forests. For. Ecol. Manage. 109, 57–74.

Johnson, P.S., Shifley, S.R., Rogers, R., 2009. The Ecology and Silviculture of Oaks, second ed. CABI International, New York, NY.

Loftis, D.L., 1990. A shelterwood method for regenerating red oak in the southern Appalachians. For. Sci. 36, 917–929.

Loftis, D.L., 2004. Upland oak regeneration and management. In: Spetich, M.A., (Ed.), Upland Oak Ecology Symposium: History, Current Conditions, and Sustainability. Gen. Tech. Rep. SRS-73. USDA Forest Service, Southern Research Station, Asheville, NC, pp. 163–167.

Lorimer, C.G., 1984. Development of the red maple understory in northeastern oak forests. For. Sci. 30, 3–22.

Lorimer, C.G., 1993. Causes of the oak regeneration problem. In: Loftis, D., McGee, C.E. (Eds.), Oak Regeneration: Serious Problems, Practical Recommendations. Gen. Tech. Rep. SE-84. USDA Forest Service, Southeastern Forest Experiment Station, Asheville, NC. pp. 14–39.

Lorimer, C.G., Chapman, J.W., Lambert, W.D., 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. J. Ecol. 82, 227–237.

Marquis, D.A., Bjorkbom, J.C., 1982. Guidelines for evaluating regeneration before and after clearcutting Allegheny Hardwoods. Res. Note NE-307. USDA Forest Service, Northeastern Forest Experiment Station, Broomall, PA, pp. 4.

Maslen, P. 1989. Response of immature oaks to prescribed fire in the North Carolina Piedmont. In: Miller, J.H., (Ed.) (Comp.), Proceedings of the 5th Biennial Southern Silvicultural Research Conference. Gen. Tech. Rep. SO-74. USDA Forest Service, Southern Forest Experiment Station, New Orleans, LA, pp. 259–266.

McEwan, R.W., Hutchinson, T.F., Ford, R.D., McCarthy, B.C., 2007. An experimental evaluation of fire history reconstruction using dendrochronology in white oak (*Quercus alba*). Can. J. For. Res. 37, 806–816.

McGee, G.G., Leopold, D.J., Nyland, R.D., 1995. Understory response to springtime prescribed fire in two New York transition oak forests. For. Ecol. Manage. 1, 149–168.

Merz, R.W., Boyce, S.G., 1956. Age of oak 'seedlings'. J. For. 54, 774–775.

Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics. John Wiley & Sons, New York.

Rebbeck, J., Gottschalk, K., Scherzer, A., 2011. Do chestnut, northern red, and white oak germinant seedlings respond similarly to light treatments? Can. J. For. Res. 41, 2219–2230.

Regelbrugge, J.C., Smith, D.W., 1994. Postfire tree mortality in relation to wildfire severity in mixed oak forests in the Blue Ridge of Virginia. Northern J. Appl. For. 11, 90–97.

Schuler, T.M., Miller, G.M., 1995. Shelterwood treatments fail to establish oak reproduction on mesic forest sites in West Virginia – 10 year results. In: Gottschalk, K.W., Fosbroke, S.L. (Eds.), Proceedings, 10th Central Hardwood Forest Conference. Gen. Tech. Rep. NE-197. Northeastern Forest Experiment Station, Radnor, PA, pp. 375–387.

Shumway, D.L., Abrams, M.D., Ruffner, C.M., 2001. A 400-year history of fire and oak recruitment in an old-growth oak forest in western Maryland, USA. Can. J. For. Res. 31, 1437–1443.

Signell, S.A., Abrams, M.D., Hovis, J.C., Henry, S.W., 2005. Impact of multiple fires on stand structure and tree regeneration in central Appalachian oak forests. For. Ecol. Manage. 218, 146–158.

Smith, K.T., Sutherland, E.K., 1999. Fire-scar formation and compartmentalization in oak. Can. J. For. Res. 29, 166–171.

Starker, T.J., 1934. Fire resistance in the forest. J. For. 33, 462–467.

Sutherland, E.K., 1997. The history of fire in a southern Ohio second-growth mixed-oak forest. In: Pallardy, S.G., Cecich, R.A., Garrett, H.E., Johnson, P.S. (Eds.), Proceedings, 11th Central Hardwoods Forest Conference. Gen. Tech. Rep. NC-188. USDA Forest Service, North Central Forest Experiment Station, St. Paul, MN, pp. 172–183.

Sutherland, E.K., Hutchinson, T.F., 2003. Characteristics of mixed-oak forest ecosystems in southern Ohio prior to the reintroduction of fire. Gen. Tech. Rep. NE-299. USDA Forest Service, Northeastern Research Station, Newtown Square, PA, pp. 159.

Sutherland, E.K., Hutchinson, T.F., Yaussy, D.A., 2003. Introduction, study area description, and experimental design. In: Sutherland, E.K., Hutchinson, T.F. (Eds.), Characteristics of Mixed-oak Forest Ecosystems in Southern Ohio Prior to the Reintroduction of Fire. Gen. Tech. Rep. NE-299. USDA Forest Service, Northeastern Research Station, Newtown Square, PA, pp. 1–16.

Whitney, G.G., 1994. From Coastal Wilderness to Fruited Plain. A History of Environmental Change in Temperate North America from 1500 to present. Cambridge University Press, Cambridge, UK.

Widmann, R.H., Balser, D., Barnett, C., Butler, B.J., Griffith, D.M., Lister, T.W., Moser, W.K., Perry, C.H., Riemann, R., Woodall, C.W., 2009. Ohio Forests, 2006. For. Serv. Resour. Bull. NRS-36. USDA Forest Service, Northern Research Station, Newtown Square, PA, pp. 119.

Yaussy, D.A., Nowacki, G.J., Schuler, T.M., Dey, D.C., DeGayner, E.J., 2008. Developing a unified monitoring and reporting system, a key to successful restoration of mixed-oak forests throughout the Central Hardwood Region. In: Deal, R.L., (Tech. Ed.), Proceedings of the 2007 National Silviculture Workshop. Gen. Tech. Rep. PNW-GTR-733. USDA Forest Service, Pacific Northwest Research Station, Portland, OR, pp. 281–285.