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Effects of fire frequency on long-term development of an oak-hickory forest in Missouri, U.S.A.

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ABSTRACT

Repeated prescribed burning over long timescales has some predictable effects on forest structure and composition, but multi-decadal patterns of stand dynamics and successional change with different fire frequencies have rarely been described. We used longitudinal data from a prescribed burning study conducted over a 63-year period to quantify stand structure (stem density, basal area, and stocking) by species group, ingrowth during the first 15 years of the study, and mortality during the first 35 years within an oak-hickory forest of the Missouri Ozarks. The study included an unburned control treatment (Control), burning with one-year return intervals (Annual), and burning with four-year return intervals (Periodic) throughout the study duration. At the stand level, stem density decreased through time across all treatments. Periodic burning increased the rate at which mortality occurred for small-diameter stems, but after 35 years, the mortality of small-diameter stems exceeded 70% across all treatments. There was little evidence of ingrowth for either burn treatment, but ingrowth increased the prevalence of non-oak species through time on the Control plots. On burned plots, basal area was maintained (Periodic) or slightly increased (Annual) during the study, primarily due to growth of trees that were present at the start of the study. However, stand stocking decreased with prescribed burning and increased in the Control plots, moving burned plots towards woodland structure while unburned plots remained as forests. Repeated burning without a fire-free interval can approximate structural conditions associated with woodlands, but suspends tree regeneration and recruitment processes necessary for canopy replacement.

1. Introduction

The structure, composition, and function of oak (*Quercus* spp.) dominated ecosystems have been strongly influenced by the fire regimes of the eastern United States (Abrams, 1992; Shumway et al., 2001; Guyette et al., 2002; Hart and Buchanan, 2011; Stambaugh et al., 2015). Information on historic fire regimes comes from several sources. A recent model of potential fire frequency, based on temperature, precipitation, and oxygen, suggests that much of the eastern United States could support mean fire return intervals <10 years (Guyette et al., 2012), with patterns in fire frequency additionally controlled by topography and human intervention (Guyette et al., 2002; Stambaugh and Guyette, 2008). Fire history reconstructions through analyses of fire scars on tree rings provide evidence of frequent, yet variable, fire regimes within oak ecosystems throughout the region (e.g., McEwan et al., 2007; Hutchinson et al., 2008; Aldrich et al., 2010). Several reconstruction studies have been conducted within the western portion of the Central Hardwoods region (e.g., Cutter and Guyette, 1994; Guyette et al., 2006; Stambaugh et al., 2015), where the prairies of the Great Plains transition to woodlands and forests, and frequent fire is understood to have contributed to the historically widespread distribution of open-forest ecosystems within this region (Nuzzo, 1986; Hanberry et al., 2012; Hanberry et al., 2014a).

Long-term studies (i.e., >25 years) demonstrate that repeated prescribed burning at frequent fire return intervals (<5 year) results in the reduction or removal of small-diameter woody vegetation and creates stands with open vertical structures in conifer (e.g., Waldrop et al., 1992; Brockway and Lewis, 1997; Haywood et al., 2001) and hardwood (e.g., DeSelm et al., 1990; Knapp et al., 2015) ecosystems. Through time, frequent fire alters tree species composition by favoring fire-tolerant species over fire-sensitive species (Glitzenstein et al., 1995; Nowacki and Abrams, 2008; Knapp et al., 2015). The reduction of tree density, especially in small-diameter classes, and the consumption of the forest floor contribute to increased abundance and diversity of herbaceous ground layer vegetation (e.g., Hiers et al., 2007; Veldman et al.,

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2014). These structural and compositional features are commonly considered defining characteristics of woodland ecosystems (Nelson, 2004; Hanberry et al., 2014b), suggesting that frequent fire is important for woodland management.

Studies over shorter time spans have had varied results regarding effects of fire on forest structure and composition. Several studies that report results within 10 years following fire events have shown few effects of prescribed burning on canopy tree mortality (e.g., Blake and Schuette, 2000; Hutchinson et al., 2005; Schwilk et al., 2009). In contrast, Elliott et al. (1999) found that one prescribed burn in the southern Appalachians significantly reduced overstory density, but effects varied with topographic position. Brose and Van Lear (1999) found that the effects of one prescribed burn on overstory trees varied by species and season of burning. Likewise, the effects of single burns on small-diameter stems vary by species, both in ability to persist without top-kill and to resprout following top-kill (Dey and Hartman, 2005; Hutchinson et al., 2005). Several studies have shown that one to three prescribed fires can be effective for favoring oak regeneration over other species (e.g., Brose et al., 1999), although not universally across the range of sites and conditions for which oak regeneration may be desirable (Brose et al., 2013). For example, Albrecht and McCarthy (2006) found that red maple (*Acer rubrum* L.) was initially top-killed by prescribed burning but recovered to outcompete oaks following harvesting in southern Ohio. Thus, the short-term effects of prescribed burning on forest structure and composition appear to vary in relation to characteristics of the fire regime or topo-edaphic conditions, whereas generalities in structural and compositional effects converge across studies over longer time scales.

Linking the short- and long-term effects of prescribed burning requires consideration of fire's effects on stand dynamics and successional development. Following disturbance, even-aged stands progress through fairly predictable stages of stand development (i.e., stand dynamics), including a period of density-dependent tree mortality driven by increased competition as individual trees grow larger (Oliver, 1980; Peet and Christensen, 1987). Through time, tree mortality shifts from a density-dependent process (i.e., the stem exclusion stage) to the outcome of local disturbances and stochastic events (i.e., the understory reinitiation stage), providing opportunities for new trees to establish and successional change to occur (Oliver, 1980). Studies describing temporal patterns of forest responses to repeated burning have generally been limited to approximately 10–15 year periods (Blankenship and Arthur, 2006; Fan et al., 2012; Hutchinson et al., 2012), whereas long-term studies more commonly report the chronic effects of different fire regimes at a single point in time (e.g., Brockway and Lewis, 1997; Haywood et al., 2001; Knapp et al., 2015). Studying the effects of prescribed burning on forest development through the stages of stand dynamics and subsequent successional change requires repeated measurement through extended periods of time.

Many land managers in the Missouri Ozarks are interested in using prescribed burning to restore woodland ecosystems on sites that historically supported frequent fire (Kabrick et al., 2014). Recently, Hanberry et al. (2014b) suggested guidelines for classifying types of forested ecosystems (i.e., savannas, open-woodlands, closed-woodlands, forests) based the Gingrich stocking chart (Gingrich, 1967), thus providing land managers with structural targets for woodland restoration. The combination of prescribed burning with timber harvest may be used to reach structural and composition targets quickly (Peterson and Reich, 2001; Kinkead et al., 2013), but the effects of only fire on forest development are not well-known. Understanding the rate of change in forest structure and composition with repeated fire would provide valuable information for developing long-term silvicultural prescriptions.

We used longitudinal data from 1950 through 2013 to describe the effects of different fire return intervals on forest development through time. Our specific objectives were to: (O1) determine effects of fire frequency on stand-level structure and composition through time; (O2) determine effects of fire frequency on the initial population of trees; and (O3) determine effects of fire frequency on rates of mortality and ingrowth during stand development. Historical documentation and pre-treatment data suggest that at the time the study started (1950), the stand was predominately a single cohort that had regenerated following widespread cutting and grazing in the early 1900s, although larger trees were also present throughout the study area. We hypothesized that: (H1) repeated prescribed burning would increase the rate of mortality of small-diameter stems, indicating acceleration through the stem exclusion stage expected in stand dynamics; and (H2) repeated prescribed burning would suspend successional changes in species composition by inhibiting regeneration and recruitment through time.

2. Methods

2.1. Study site and experimental design

A long-term burning study was established in 1949 at University Forest Conservation Area in Butler County, MO (~36°54′ N, 90° 19′W), within the Black River Ozark Border Subsection of the Ozark Highlands Ecological Section (Nigh and Schroeder, 2002). The study area has moderately well-drained, upland soils formed in loess, with a fragipan that impedes drainage at a moderate depth. Soils include Loring silt loam soil series (fine-silty, mixed, active, thermic oxyaquic Fragiudalf) and Captina silt loam soil series (fine-silty, siliceous, active, mesic typic Fradiudult) (Graves, 1984). Both soil series have silt loam at the surface, but the Captina soil series has silty clay loam from 13 to 64 cm and cherty limestone residuum beneath. Since 1949, with the exception of missing data from 2000 and 2001, mean temperature at the Wappapello Dam climate station (36°55′ N, 90°17′ W) was 14.4 °C and mean precipitation was 113 cm (National Climatic Data Center). Dominant trees on the site were characteristic of oak-hickory forests in this region and included post oak (*Quercus stellata* Wangenh.), scarlet oak (*Quercus coccinea* Muenchh.), black oak (*Quercus velutina* Lam.), southern red oak (*Quercus falcata* Michx.), and hickories (*Carya* spp.) (Paulsell, 1957).

The study initially included just one replicate of all treatments, but the addition of a second replicate in 1951 created two blocks in a randomized complete block design. Each block consisted of six plots, and each plot measured 40 × 40 m, with a 10 m buffer around all sides. The study included three treatments that were each randomly assigned to two plots in each block: an unburned control (Control); annual prescribed fire, with one-year fire return intervals (Annual); and periodic prescribed fire, with four-year fire return intervals (Periodic). Treatment application began in 1949 in one block and in 1951 in the other block, staggering the application of the Periodic treatment in the separate blocks throughout the duration of the study. All burns were conducted between March and May. Prior to 1988, the study area was owned by the University of Missouri, and the prescribed burns were conducted by university personnel. The Missouri Department of Conservation (MDC) purchased the property in 1988, and the prescribed burning treatments were continued by MDC foresters. Although each block included two plots for each treatment, the two Annual plots and the two Periodic plots within each block were burned with a single fire and were therefore considered to be the same experimental unit for analyses.

2.2. Data collection

Prior to treatment application, all trees ⩾4 cm diameter at breast height (DBH) were tagged with aluminum tags, and species and DBH were recorded for each tree. Although the two blocks were established in different years (1949 and 1951), we refer to the pre-treatment data as collected in 1950 for both blocks in this study. Study plots were re-measured for DBH and species in 1964, 1972, 1984, and 2013, although there were notable differences in sampling methods in the different years. Sampling in 1964 followed the same methodology as that in 1950, with all trees ⩾4 cm DBH measured, including individuals that grew larger than the minimum size threshold during that period (i.e., ingrowth). In 1972 and 1984, all trees that had previously been tagged in 1950 or 1964 were measured for DBH, but ingrowth was not included in the re-measurement. By 2013, many of the tags remained present but were illegible, so all trees ⩾10 cm DBH were tagged with new aluminum tags, and species and DBH were recorded for each tree. In addition, the DBH of each tree >1.37 m tall and <10 cm DBH was recorded by species in five circular sub-plots (5.65 m radius; 0.01 ha) that were systematically established in each plot. One sub-plot was located at plot center, and each of the other four sub-plots was halfway between plot center and each respective plot corner. On sub-plots with very high stem densities (n = 4 out of 60), we reduced the sub-plot size to 0.005 ha (4 m radius) to make sampling more efficient.

2.3. Data analysis

Due to the different sampling methodologies through time, we separated data into two datasets for analyses. Dataset 1 (referred to as 'stand-level') consisted of stand-level data on trees ⩾4 cm DBH and included years 1950, 1964, and 2013, from which we produced diameter distributions for each treatment, compared stand-level metrics (basal area, stem density, and stocking) through time, and evaluated ingrowth from 1950 to 1964. We were unable to evaluate ingrowth after 1964 because it was not recorded in 1972 and 1984, and we could not determine if original tags were missing in Control plots in 2013. We then used only trees that were present in 1950 for Dataset 2 (referred to as '1950 population'), and we quantified effects of study treatments on mortality and changes in structural and compositional characteristics of the 1950 population through 1984. We were unable to assess the mortality of the 1950 population in 2013 because many original tags were illegible. For each dataset, we report response variables for all trees and by the following species groups: white oaks (*Quercus alba* L., *Q. stellata*), red oaks (*Q. coccinea*, *Q. falcata*, *Q. velutina*), hickories (*Carya glabra* (Mill) Sweet, *C. texana* Buckley, *C. tomentosa* (Lam.) Nutt.), and other species (e.g., *Cornus florida* L., *Nyssa sylvatica* Marschall, *Ulmus alata* Michx.).

For both datasets, we calculated basal area (m^2/ha) and stem density (trees per hectare) for all trees and by species group and used mixed-model repeated measures Analysis of Variance (ANOVA) to test for effects of treatment and time on response variables. We used a random block effect and a first order autoregressive covariance structure for the repeated measures matrix. For significant treatment by time interaction effects, we tested for significance of each effect within each level of the interacting effect. We used the Tukey's Honestly Significant Difference (HSD) adjustment for all pair-wise comparisons, with p-values presented in the text. In the absence of significant treatment by time interaction effects, we report marginal means with pair-wise comparisons for each effect.

For the time period from 1950 to 1964, we used the stand-level dataset (Dataset 1) to determine the stem density by species for the ingrowth population. We used ANOVA with a random block effect to test for treatment effects on ingrowth, using Tukey's HSD for all pair-wise comparisons. To describe rates of mortality, we used the 1950 population (Dataset 2) to calculate the percentage of the 1950 population that was recorded as dead in 1964, 1972, and 1984 by 2-cm diameter classes and compared the complete 1950 diameter distribution to the diameter distribution of 1950 trees that were still alive in 1984.

3. Results

3.1. Stand-level responses (Dataset 1)

Diameter distributions in 1950 displayed the 'reverse-J' pattern for each treatment (Fig. 1A), with abundant trees in small size classes but trees also present across size classes up to 60 cm. By

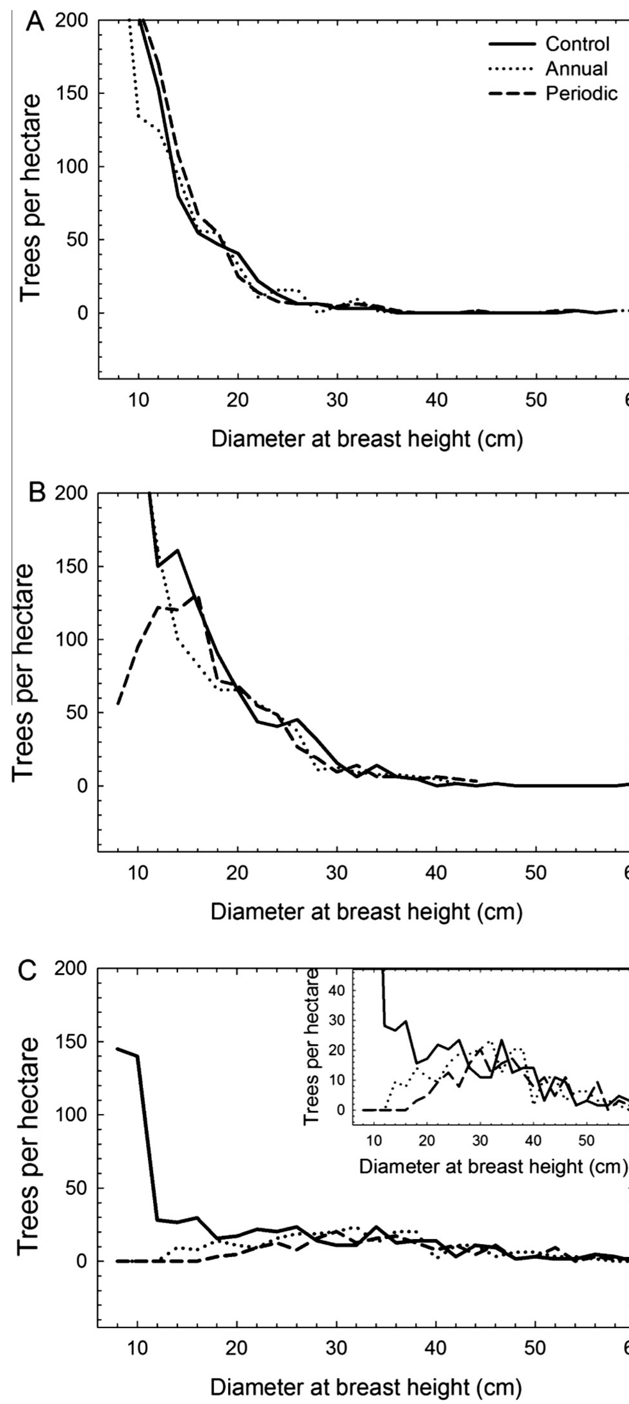

Fig. 1. Diameter distributions by treatment in (A) 1950, (B) 1964, and (C) 2013. All trees >4 cm were measured but size classes ⩾8 cm are displayed to limit the scale of the y-axis and show greater detail for larger diameter classes. Inset in Panel C reduces the scale on the y-axis to show greater detail for the 2013 distributions.

1964, the primary treatment effect on diameter distributions was a notable reduction in small stems (approximately <12 cm) in the Periodic plots, with few observable differences in the diameter distributions for Control and Annual plots (Fig. 1B). By 2013, the Annual and Periodic plots had unimodal diameter distributions, and the Control plot approximated a reverse-J, with substantial increases in stem densities below 10 cm diameter classes (Fig. 1C). Based on Gingrich (1967), total stand stocking was between 75 and 80 percent for all treatments at the start of the study (Fig. 2). Stocking increased on the Control plots to near 100 percent in 2013, whereas stand stocking was reduced through time with prescribed burning. By 2013, stand stocking was about 70 percent on Annual plots and about 60 percent on Periodic plots (Fig. 2).

There was a significant interaction between treatment and time effects on stand-level basal area for all species combined (Table 1). In the Control plots, basal area increased from 1950 to 1964 ($p = 0.020$) and from 1964 to 2013 ($p = 0.004$) (Fig. 3A). In Annual plots, there was no difference in basal area between 1950 and 1964 ($p = 0.924$), but basal area was greater in 2013 than in 1964 ($p = 0.009$) or in 1950 ($p = 0.002$). Basal area did not change through time in Periodic plots. In 1950, there were no differences in total basal area among the treatments ($p = 0.796$). In 1964 and 2013, Control plots had greater basal area than the Annual ($p = 0.015$, $p < 0.001$, respectively) and the Periodic ($p = 0.041$, $p < 0.001$, respectively), and Annual plots had greater basal area than Periodic plots in 2013 ($p = 0.032$) (Fig. 3A). Among the species groups, there were no significant interactions between treatment and time effects on stand-level basal area (Table 1; Fig. 4), and therefore marginal means are provided for each treatment or year effect (Table 2). The basal area of white oaks was greater in 2013 than in 1950 ($p = 0.003$) or in 1964 ($p = 0.023$), but did not differ between 1950 and 1964 ($p = 0.297$). The basal area of hickories was lower in 2013 than in 1950 ($p = 0.020$) and in 1964 ($p = 0.003$). The only significant effect of treatment was on hickories, with significantly greater basal area on Control plots than on Annual plots ($p = 0.038$) (Table 2).

Stem densities decreased through time regardless of treatment, with significantly more trees per hectare in 1950 than in 1964 ($p = 0.004$) or 2013 ($p < 0.001$) and significantly more trees in 1964 than in 2013 ($p = 0.001$) (Table 2). There was no significant interaction between treatment and time effects on stem densities of all species combined (Table 1; Fig. 3B). There were significantly more trees in Control plots than in Periodic plots ($p = 0.008$) (Table 2). Among the species groups, there was a significant interaction between treatment and time effects for only the ‘other’

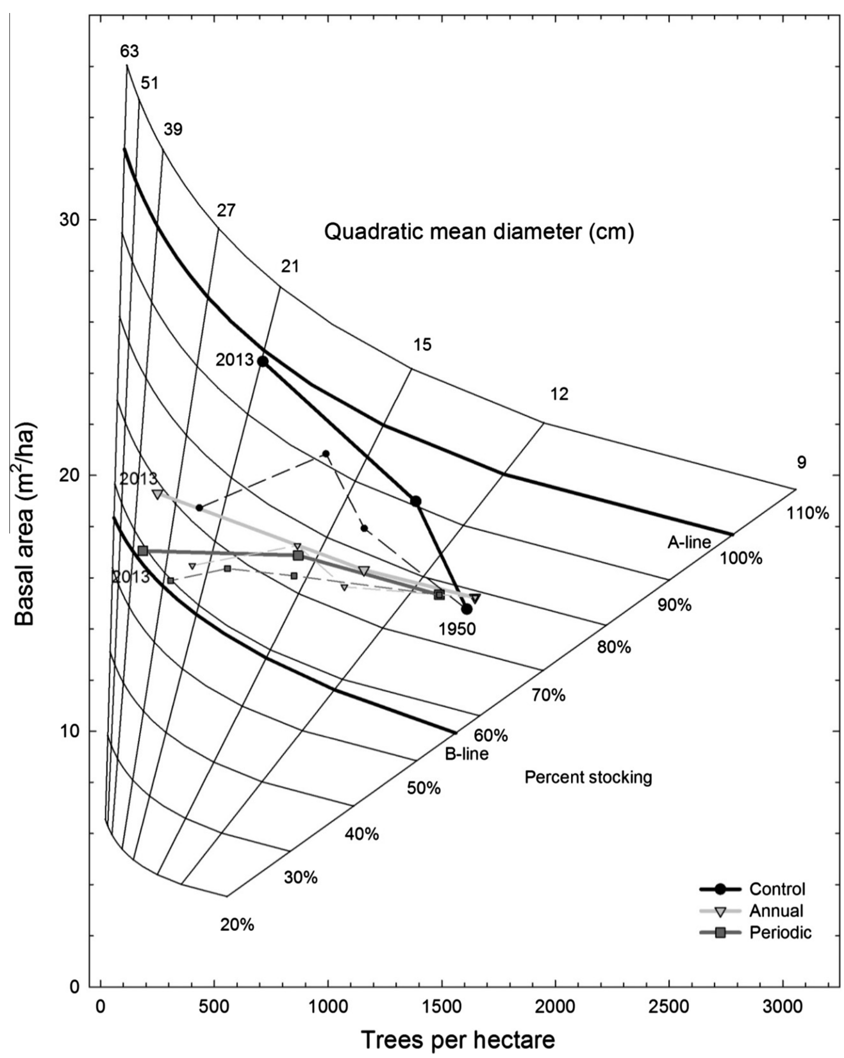

Fig. 2. Stand structural characteristics plotted on a Gingrich stocking chart for each treatment and measurement year. Solid lines are from stand-level data (Dataset 1) and points include 1950, 1964, and 2013. Dashed lines with the same symbol type are the values for the 1950 population only (Dataset 2) and points include 1950, 1964, 1972, and 1984. Only points in 1950 and 2013 are labeled for legibility.

Table 1
Results of repeated measures ANOVA tests for treatment (trt), year, and trt ∗ year interaction effects on basal area (m^2/ha) and stem density (trees per hectare) for all species and selected species groups for stand-level data from 1950, 1964, and 2013 (Dataset 1).

Species group	Variable	Basal area (m^2/ha)				Trees per hectare			
		Num DF	Den DF	F value	p-value	Num DF	Den DF	F value	p-value
All species	trt	2	8	20.19	0.001	2	8	8.70	0.010
	year	2	8	53.14	<0.001	2	8	84.14	<0.001
	trt ∗ year	4	8	11.77	0.002	4	8	1.64	0.256
White oaks	trt	2	8	1.13	0.371	2	8	0.69	0.530
	year	2	8	12.91	0.003	2	8	13.43	0.003
	trt ∗ year	4	8	0.18	0.941	4	8	0.14	0.962
Red oaks	trt	2	8	1.68	0.245	2	8	3.18	0.096
	year	2	8	0.73	0.513	2	8	45.09	<0.001
	trt ∗ year	4	8	0.83	0.543	4	8	0.81	0.551
Hickories	trt	2	8	5.39	0.032	2	8	10.41	0.006
	year	2	8	12.49	0.006	2	8	105.18	<0.001
	trt ∗ year	4	8	0.56	0.702	4	8	3.68	0.055
Other species	trt	2	8	4.04	0.061	2	8	116.92	<0.001
	year	2	8	0.51	0.621	2	8	59.83	<0.001
	trt ∗ year	4	8	3.38	0.067	4	8	99.83	<0.001

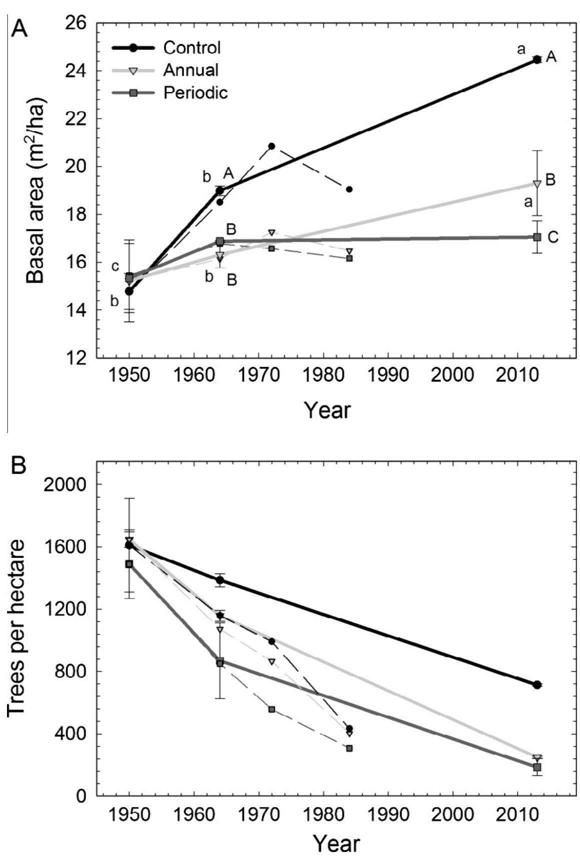

Fig. 3. Changes in (A) basal area (m^2/ha) and (B) stem density (trees per hectare) through time by treatment. Solid lines are for stand-level data (Dataset 1) and points include 1950, 1964, and 2013. Dashed lines are the values for the 1950 population only (Dataset 2) and points include 1950, 1964, 1972, and 1984. Standard errors are shown for only Dataset 1 to increase the legibility of the figure. For significant year ∗ treatment interactions (see Tables 1 and 3), the same letter indicates no significant difference within each respective treatment; capital letters represent pair-wise comparisons among treatments within years and lower-case letters represent pair-wise comparisons among years within treatments. With no significant interaction, marginal means are shown in Tables 2 and 4.

species group (Table 1; Fig. 5D). Stem density for 'other' species was significantly greater in 2013 than in 1950 ($p < 0.001$) or 1964 ($p < 0.001$) for Control plots but did not differ across years for Annual or Periodic plots. In 2013, stem density of 'other' species was significantly greater for Control plots than for Annual ($p < 0.001$) and Periodic ($p < 0.001$) plots (Fig. 5D). Stem densities for white oaks, red oaks, and hickories decreased through time regardless of the treatment (Table 2). The only species group with a significant treatment effect on stand-level stem density was hickories, with greater stem density in Control plots than in Annual ($p = 0.045$) or in Periodic ($p = 0.005$) plots (Table 2).

Despite relatively large numerical differences in stem densities among treatments for ingrowth from 1950 to 1964, there were no significant treatment effects for ingrowth across all species combined (Fig. 6). In the Control plots, there were 227 ingrowth trees per hectare in 1964, compared to 86 and 16 ingrowth trees per hectare in Annual and Periodic plots, respectively. The ingrowth in Annual plots was dominated by hickories, whereas ingrowth was fairly evenly distributed among white oaks, red oaks, and hickories in Control plots, with a greater abundance of 'other' species in Controls than in burned treatments (Fig. 6).

3.2. The 1950 population (Dataset 2)

There was a significant interaction between treatment and year effects on the basal area of the 1950 population (Table 3). Basal area did not significantly differ among years for Annual ($p = 0.153$) or Periodic ($p = 0.694$) plots (Fig. 3A). In Control plots, basal area increased through time, with lower basal area in 1950 than in 1972 ($p = 0.001$) or in 1984 ($p = 0.023$). In 1972 and 1984, the Control plots had greater basal areas than the Annual ($p = 0.044$, $p = 0.025$, respectively) and Periodic ($p = 0.010$, $p = 0.008$, respectively). Regardless of treatment, the basal area of white oaks increased through time and was greater in 1972 ($p = 0.040$) and in 1984 ($p = 0.020$) than in 1950 (Table 4). In contrast, hickories had lower basal area in 1984 than in 1950 ($p = 0.015$), 1964 ($p = 0.003$), and 1972 ($p = 0.014$). Hickories had significantly greater basal area in Control plots than in Annual ($p = 0.031$) and in Periodic ($p = 0.045$) plots (Table 4).

There was no significant interaction between treatment and year for stem densities of the 1950 population (Table 3; Fig. 3B). The Periodic treatment had fewer trees per hectare than the Control ($p = 0.014$) or Annual ($p = 0.047$) treatment, and stem densities consistently decreased through time for all treatments (Table 4). For the 1950 population, there were no significant interactions between treatment and time effects for any species groups (Table 3; Fig. 5). Based on marginal means, stem densities significantly decreased through time for all species groups (Table 4). There were fewer hickories in Periodic plots than in Control

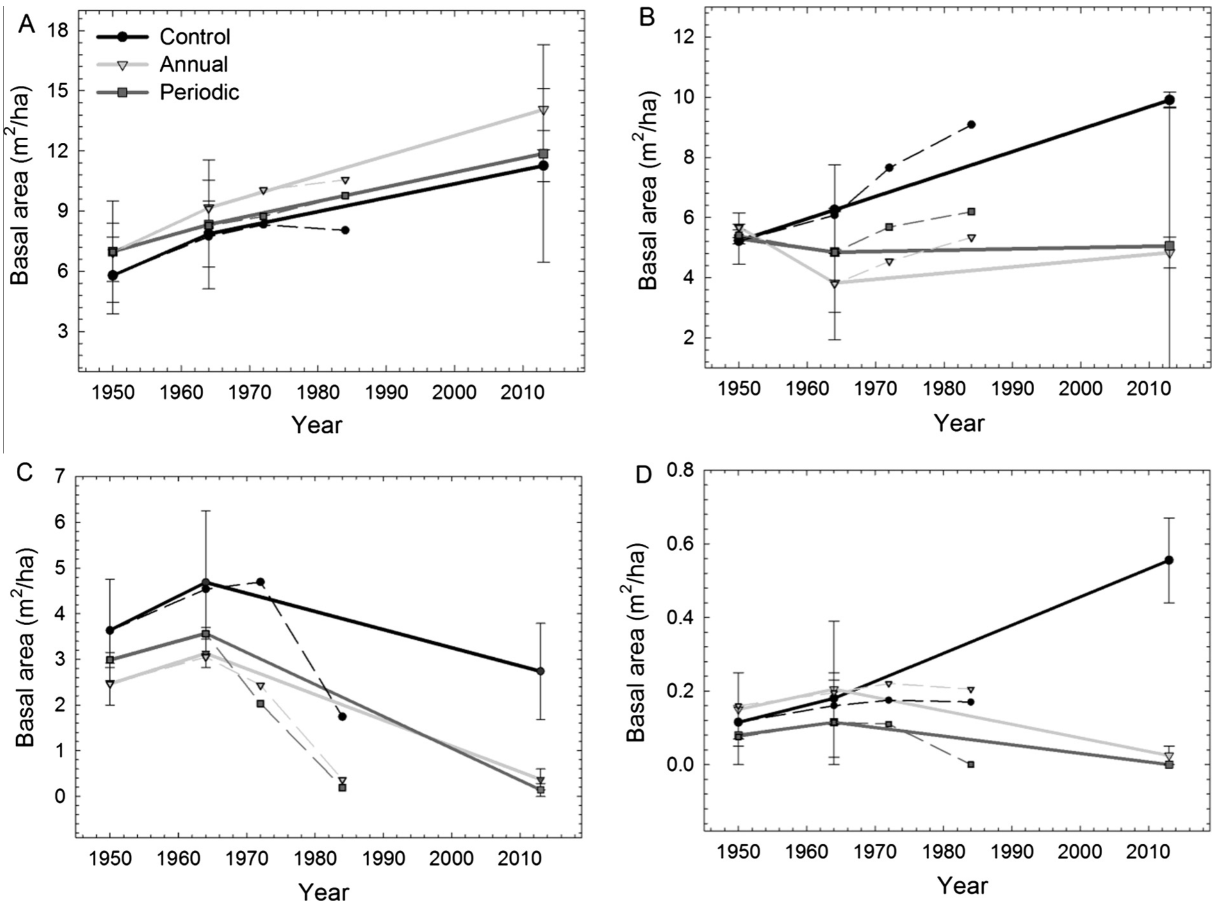

Fig. 4. Changes in basal area (m^2/ha) through time by treatment for (A) white oak species, (B) red oak species, (C) hickory species, and (D) other species. Solid lines are for stand-level data (Dataset 1) and points include 1950, 1964, and 2013. Dashed lines are the values for the 1950 population only (Dataset 2) and points include 1950, 1964, 1972, and 1984. Standard errors are shown for only Dataset 1 to increase the legibility of the figure. With no significant interaction, marginal means are shown in Tables 2 and 4.

Table 2
Marginal means and standard errors of basal area (m^2/ha) and stem density (trees per hectare) by treatment and year for each species group using stand-level data from 1950, 1964, and 2013 (Dataset 1). The same superscript letter indicates no significant difference between treatment levels within a species group for significant treatment (lower case letters) or year effects (capital letters).

Species group	Control		Annual		Periodic		1950		1964		2013	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Basal area (m²/ha)												
All species*	.	.	.	.	.	.	.	.	.	.	.	.
White oaks	8.3	1.2	10.1	1.5	9.1	2.0	6.6^B	0.9	8.5^B	1.0	12.4^A	1.5
Red oaks	7.1	0.9	4.8	0.4	5.1	1.4	5.4	0.2	5.0	0.9	6.6	1.6
Hickories	3.7^a	0.7	2.0^b	0.5	2.2^{ab}	0.7	3.0^A	0.4	3.8^A	0.5	1.1^B	0.6
Other species	0.3	0.1	0.1	0.1	0.1	0.0	0.1	0.0	0.2	0.1	0.2	0.1
Trees per hectare												
Total	1237^a	188	1018^{ab}	259	848^b	253	1582^A	102	1137^B	115	383^C	106
White oaks	510	111	474	99	403	144	673^A	113	513^A	84	200^B	31
Red oaks	290	72	236	92	184	78	452^A	51	204^B	44	55^C	13
Hickories	380^a	50	299^b	93	255^b	83	446^A	23	407^A	30	81^B	45
Other species*	.	.	.	.	.	.	.	.	.	.	.	.

* Marginal means are not displayed due to significant treatment ∗ year interactions (see Table 1).

(p = 0.004) or in Annual (p = 0.049) plots, and the Control plots had more red oaks per hectare than the Periodic plots (p = 0.021).

The proportion of the 1950 population that had died by 1964 was generally greater for small-diameter trees in Periodic plots than in Annual or Control plots (Fig. 7). This trend was also apparent for trees that had died by 1972. However, by 1984 at least 70 percent of the 1950 population had died for trees <10 cm DBH, regardless of treatment. Within the Periodic plots, >95 percent of the small-diameter 1950 population had died by 1984. From the initial 1950 population, the trees that remained alive in 1984 had similar diameter distributions in 1950 for Control and Annual plots but showed higher mortality of small-diameter stems from 1950 to 1984 for Periodic plots (Fig. 7D).

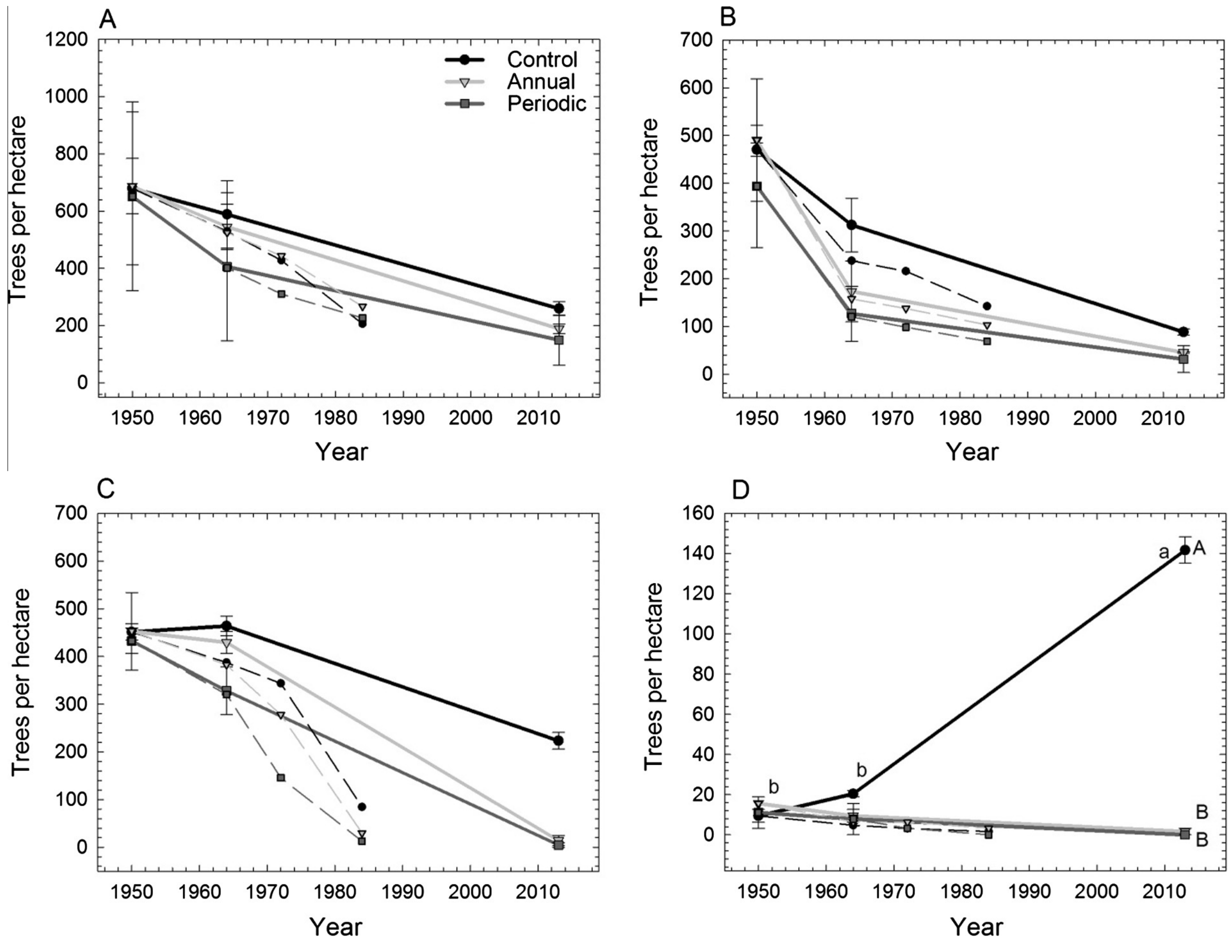

Fig. 5. Changes in stem density (trees per hectare) through time by treatment for (A) white oak species, (B) red oak species, (C) hickory species, and (D) other species. Solid lines are for stand-level data (Dataset 1) and points include 1950, 1964, and 2013. Dashed lines are the values for the 1950 population only (Dataset 2) and points include 1950, 1964, 1972, and 1984. Standard errors are shown for only Dataset 1 to increase the legibility of the figure. For significant year ∗ treatment interactions (see Tables 1 and 3), the same letter indicates no significant difference within each respective treatment; capital letters represent pair-wise comparisons among treatments within years and lower-case letters represent pair-wise comparisons among years within treatments. With no significant interaction, marginal means are shown in Tables 2 and 4.

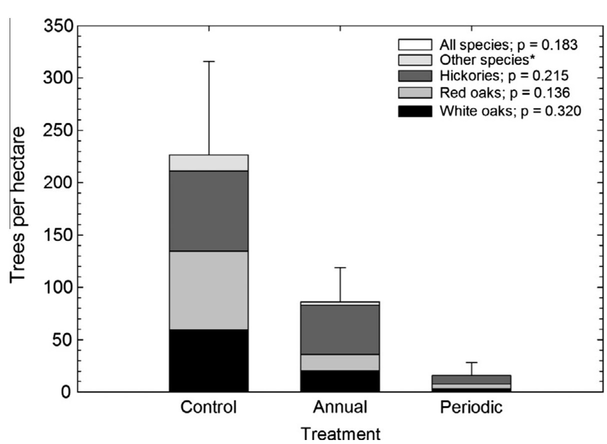

Fig. 6. Stem densities of the 1964 ingrowth (i.e., trees to have entered the size class ⩾4 cm diameter at breast height between 1950 and 1964) by treatment and species group. *no stems were present in Annual or Periodic plots.

4. Discussion

Patterns of forest development are dependent on the legacies of the past. At the start of the study, forest structure and composition were similar among the study treatments and included a predominance of white oak species, followed by red oak species, hickories, and very few trees of other species. At that time, the study area was described as a ''moderately well-stocked, all-aged stand of the oak-hickory type on an upland 'flatwoods''', with no grazing in the area for the preceding 10–15 years and no fire for around 20 years (Paulsell, 1957). The diameter distributions in 1950 followed the 'reverse-J' shape (Fig. 1) common to uneven-aged forests and appear similar to that of an uneven-aged oak-hickory forest managed with single-tree selection in the Missouri Ozarks (Loewenstein et al., 2000). However, in contrast to typical uneven-age forest structure, in which greater proportions of stand basal area are in larger trees (Loewenstein, 2005), we found that trees less than 25.4 cm DBH accounted for 81 percent of stand basal area at the start of the study. Given the history of timber exploitation and land use in the Ozarks (Guldin, 2008), it is likely that timber in the study area was selectively cut at the turn of the 20th century, resulting in a largely even-aged stand with scattered trees in the canopy left over from the logging.

4.1. Fire effects on stand dynamics

During the study period, we observed reductions in stem densities consistent with self-thinning, but the increased rate of mortality of small trees on Periodic plots supported the hypothesis that prescribed burning accelerated the rate of stand development through stem exclusion (H1). The number of trees that a site can

Table 3
Results of repeated measures ANOVA tests for treatment (trt), year, and trt ∗ year interaction effects on basal area (m^2/ha) and stem density (trees per hectare) for all species and selected species groups for the 1950 population in 1950, 1964, 1972, and 1984 (Dataset 2).

Species group	Variable	Basal area (m^2/ha)				Trees per hectare			
		Num DF	Den DF	F value	p-value	Num DF	Den DF	F value	p-value
All species	trt	2	11	14.68	0.001	2	11	6.67	0.013
	year	3	11	12.62	0.001	3	11	73.31	<0.001
	trt ∗ year	6	11	3.42	0.037	6	11	0.59	0.735
White oaks	trt	2	11	3.38	0.072	2	11	0.78	0.482
	year	3	11	5.08	0.019	3	11	10.43	0.002
	trt ∗ year	6	11	0.26	0.946	6	11	0.15	0.985
Red oaks	trt	2	11	2.45	0.131	2	11	5.20	0.026
	year	3	11	1.13	0.381	3	11	41.59	<0.001
	trt ∗ year	6	11	0.46	0.827	6	11	0.35	0.898
Hickories	trt	2	11	5.51	0.022	2	11	8.84	0.005
	year	3	11	8.62	0.003	3	11	98.97	<0.001
	trt ∗ year	6	11	0.38	0.879	6	11	1.79	0.190
Other species	trt	2	11	0.94	0.421	2	11	0.85	0.453
	year	3	11	0.11	0.954	3	11	4.75	0.023
	trt ∗ year	6	11	0.07	0.998	6	11	0.21	0.964

Table 4
Marginal means and standard errors of basal area (m^2/ha) and stem density (trees per hectare) by treatment and year for each species group using data from the 1950 population in 1950, 1964, 1972, and 1984 (Dataset 2). The same superscript letter indicates no significant difference between treatment levels within a species group for significant treatment (lower case letters) or year effects (capital letters).

Species group	Control		Annual		Periodic		1950		1964		1972		1984	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Basal area (m^2/ha)														
All species*	.	.	.	.	.	.	.	.	.	.	.	.	.	.
White oaks	7.3	0.7	9.1	0.7	8.4	1.3	6.6^{B}	0.9	8.1^{B}	1.0	9.0^{AB}	1.1	9.4^{A}	1.3
Red oaks	7.0	0.6	4.8	0.4	5.3	1.1	5.4	0.2	4.7	0.8	5.9	1.0	6.8	1.3
Hickories	3.6^{a}	0.7	2.1^{b}	0.4	2.2^{b}	0.5	3.0^{A}	0.4	3.6^{A}	0.5	3.1^{A}	0.7	0.8^{B}	0.4
Other species	0.2	0.0	0.2	0.1	0.1	0.0	0.1	0.0	0.2	0.1	0.2	0.1	0.1	0.1
Trees per hectare														
All species	1049^{a}	171	997^{a}	170	801^{b}	183	1582^{A}	102	1027^{B}	92	805^{BC}	101	382^{C}	37
White oaks	461	89	481	64	398	110	673^{A}	113	485^{AB}	84	394^{BC}	67	233^{C}	41
Red oaks	266^{a}	47	222^{ab}	66	170^{b}	57	452^{A}	51	172^{B}	32	151^{B}	29	105^{B}	19
Hickories	317^{a}	53	286^{a}	64	228^{b}	63	446^{A}	23	364^{B}	22	256^{C}	41	42^{D}	15
Other species*	5	1	8	2	5	3	12^{A}	2	6^{AB}	2	4^{AB}	1	2^{B}	1

* Marginal means are not displayed due to significant treatment ∗ year interactions (see Table 3).

support is related to the size of those trees (Reineke, 1933), allowing for predictability in density-dependent mortality as stands age and trees grow larger (Peet and Christensen, 1987; Williams, 2003). Temporal patterns in stem densities of the 1950 population (Dataset 2) converged among treatments by 1984 for all species combined and for each species group, suggesting that long-term mortality patterns within unburned stands (through density-dependent mortality or other mortality processes) were similar to those in stands with repeated burning. These findings were further supported by the distributions of mortality by size class, which showed nearly complete mortality of small-diameter (<10 cm DBH) stems by 1984 in all study treatments, including Controls. Prescribed burning in Periodic plots had a 'thin from below' effect, in which small-diameter stems were eliminated from the 1950 population more rapidly than in Annual or Control plots, but similar sized stems eventually died without fire.

The more rapid rate of mortality of small-diameter trees on Periodic plots than Annual plots was likely due to differences in fire behavior. Following the first burns at the initiation of the study, fuel loading on the Annual plots was likely lower than that in Periodic plots due to time required to accumulate surface fuels. Stambaugh et al. (2006) reported that it takes between 3 and 4 years to accumulate 75% of pre-burn litter loads in Missouri Ozark forests, with only 25% of pre-burn fuel loads accumulated after one year. Hardwood litter fuel loads have been positively associated with fire intensity in oak-hickory forests (Graham and McCarthy, 2006). Thus, lower fuel loads in Annual plots may have reduced the fire intensity of subsequent burns, while repeated annual burning kept fuel loads low for the duration of the study. Greater fire intensity increases the likelihood of tissue necrosis and subsequent tree mortality (Bova and Dickinson, 2005; Stephan et al., 2010) and likely increased mortality rates on Periodic plots.

The low number of small-diameter trees that survived from 1950 to 1984 across all treatments may also have been associated with initial stand structure, which included trees across a wide range of size classes. The development of these stands may have differed from a true even-aged cohort in that some of the growing space was initially occupied by larger trees in competitively dominant positions. It is likely that the competitive advantage of the larger trees contributed to their persistence during the density-dependent mortality stage of stand development. Further, tree size is positively related to the probability of survival following fire (Dey and Hartman, 2005), suggesting that the larger trees at the start of the study were less vulnerable to both fire-induced and competition-induced mortality.

4.2. Fire effects on forest succession

Our results support the hypothesis that repeated prescribed burning suspended successional development by inhibiting

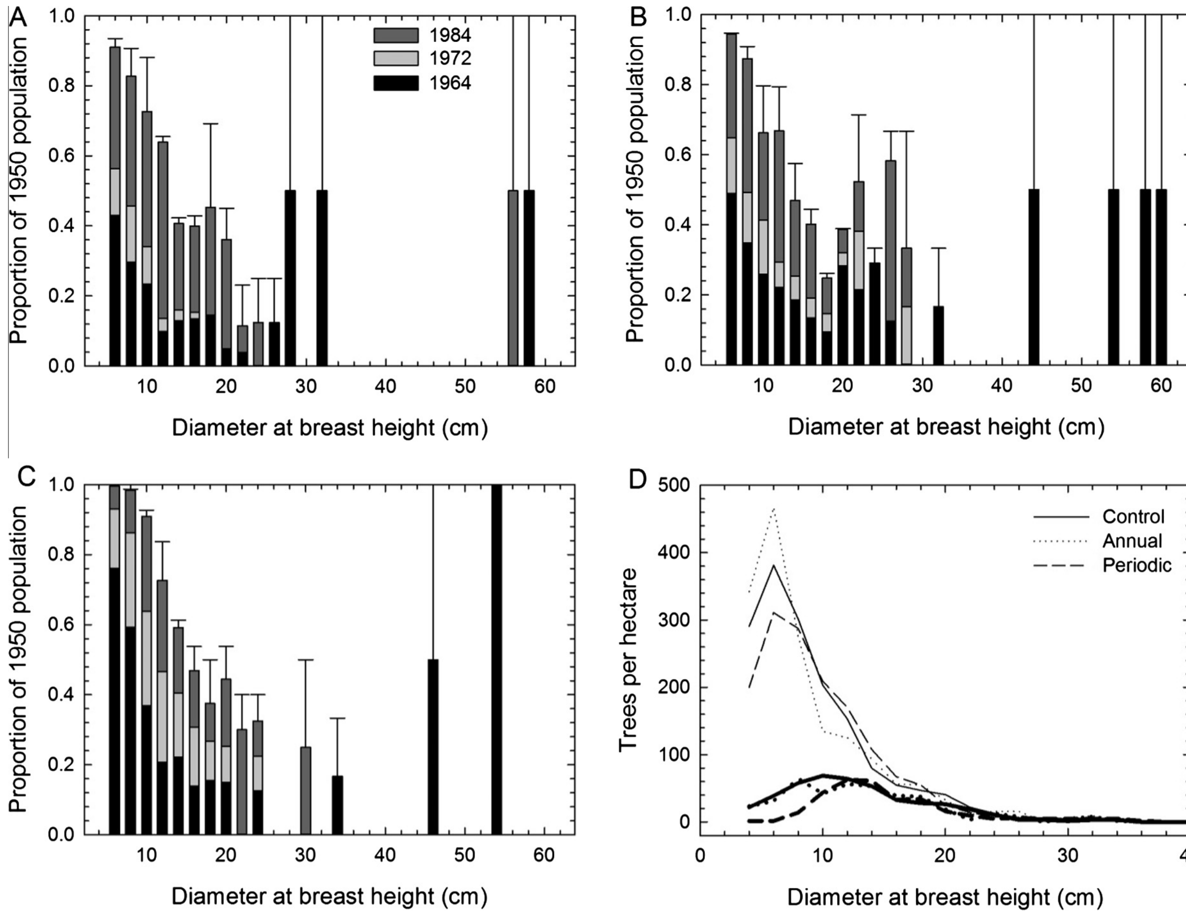

Fig. 7. Mortality distributions of the 1950 population of trees >4 cm diameter at breast height showing the proportion of trees to have died by 1964, 1972, and 1984 for (A) Control plots, (B) Annual plots, and (C) Periodic plots, and (D) diameter distribution of the 1950 population (thin lines) and diameter distributions of the subset of the 1950 population that remained alive in 1984 (thick lines).

regeneration/recruitment processes that occurred in the unburned Control (H2). A complete understanding of tree turnover through time was limited, because ingrowth was not quantified following the 1964 measurement period. However, several lines of evidence indicate that ingrowth did not contribute to stand development within either burn treatment, but was an important contributor in Control plots. First, differences in stem densities between the stand-level dataset and the 1950 population dataset within each treatment in 1964 (Fig. 3B and Fig. 5) represent ingrowth that occurred between 1950 and 1964, with little difference between datasets in burn treatments. Second, comparing stem densities in 1984 from the 1950 population to those in 2013 from the stand-level dataset suggests continued attrition within both burn treatments, whereas the greater stem densities in 2013 than in 1984 in Control plots is possible only due to ingrowth. Third, field observations in 2013 indicated that no trees ⩾4 cm DBH had established after 1964 in either burn treatment, because all trees had evidence of a previously established tag (although many were illegible). Finally, the diameter distributions from 2013 demonstrate that the burn treatments essentially eliminated all small diameter stems, and the Control plots included abundant small-diameter stems (see also Knapp et al., 2015).

The increase in abundance of trees in the 'other' species group on Control plots suggests that ingrowth is initiating a potential shift in species composition through succession. Fire has been widely discussed as an important disturbance for establishing and maintaining oak ecosystems in the eastern U.S., with reductions in fire frequency contributing to successional changes to non-oak species (Nowacki and Abrams, 2008; McEwan et al., 2011; Arthur et al., 2012; Brose et al., 2013). Although oak regeneration problems are relatively uncommon in the Missouri Ozarks, where site conditions are more xeric and other species are less competitive than in forests further east, recent research suggests that successional changes in forest composition may be occurring in the Ozarks as well (Olson et al., 2014).

Repeated burning suspended successional shifts in forest composition by eliminating ingrowth but also prohibited the recruitment of oak/hickory stems from the regeneration layer to the overstory. Annual burning eliminated nearly all seedlings and saplings, but oaks and hickories remained the dominant tree species in the sapling layer on Periodic plots in 2013 via resprouting (Knapp et al., 2015). These findings demonstrate the need for a fire-free interval for successful oak recruitment. Fire-free periods have been incorporated into silvicultural prescriptions for oak regeneration (e.g., Brose et al., 1999), with recommended durations of 10–30 years depending on site quality and stand conditions (Arthur et al., 2012).

4.3. Fire effects on stand structure and composition through time

The temporal patterns of stand-level basal area and stocking are influenced by both tree number and tree size (growth) and thus were likely attributable to different processes in burned compared to unburned plots. Stand-level basal area did not change through time on the Periodic plots, suggesting that losses to basal area through tree mortality were balanced by growth of the remaining

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population. On Annual plots, stand-level basal area increased slightly through time and was significantly greater than that in Periodic plots. However, we cannot definitively conclude if differences were due to differences in growth rates of residual trees between the two burn treatments or due to undetected differences in tree mortality. In contrast to the burn treatments, the increase in basal area in the Control plots is likely due to a combination of growth of the original population and continued ingrowth through time, with apparent increases in basal area of each species group except hickories.

Our results demonstrate several possible differences in effects of prescribed burning among species groups common to the Central Hardwood forest region. For example, prescribed burning reduced the abundance of hickories in comparison to the Control plots, both at the stand level and also in the 1950 population of trees. In contrast, Fan et al. (2012) reported that hickories had relatively high rates of survival through 10 years of burning due to morphological characteristics. We suspect that differences in our results may be associated with either the cumulative effects of burning for longer time periods or differences in the size distributions of the populations studied. We also found that there were no effects of treatment on stem densities of white oak species, whereas stem densities of red oak species were reduced with burning. The white oak species group was dominated by post oak, a relatively fire-tolerant species in our study (Huddle and Pallardy, 1996). Through time, the continued mortality of hickories and red oak species resulted in contemporary forests dominated by post oak in the burned plots (Knapp et al., 2015).

5. Management implications

Forest managers commonly use stocking charts to guide prescriptions for stand structure (Gingrich, 1967; Kabrick et al., 2014), and recently, Hanberry et al. (2014b) recommended stocking targets for oak savanna (<30% stocking), open oak woodland (30–55% stocking), closed oak woodland (55–75% stocking) and oak forest (>75% stocking) conditions. Accordingly, the study plots would all have been classified as oak forests at study initiation. In 2013, Control plots were near 100% stocking and remained an oak-hickory forest, but both burn treatments created closed woodlands by 2013. Although the Periodic treatment resulted in greater mortality than Controls in the first few decades of the study, mortality was predominantly within small-diameter stems, and stocking levels did not appreciably decrease in the first 14 years. Managers wishing to increase the rate of change in forest structure may consider thinning treatments to remove large-diameter trees and more rapidly reach stocking targets.

This study provides unique insights into both short- and long-term effects of fire on an oak-hickory forest ecosystem. Repeated prescribed burning affected stand structure in the short-term through mortality of primarily small-diameter stems. However, stems within the same small-diameter size classes on unburned Controls also succumbed to mortality within approximately 35 years, suggesting that repeated prescribed burning accelerated natural mortality processes by killing small trees. Prescribed fire increased the basal area of the more fire-tolerant white oaks (predominantly post oak) but decreased the basal area of less fire-tolerant red oaks and hickories. Long-term differences in stand composition and structure were primarily attributed to repeated fire inhibiting ingrowth, which resulted in compositional shifts to non-oak species in small size classes on Control plots. This study confirms that long-term, repeated prescribed burning can create and maintain structural characteristics associated with woodlands, but the time required for woodland development may exceed that desired for restoration. In addition, the elimination of ingrowth introduces a potential regeneration challenge if canopy cover is desired in perpetuity, suggesting that a fire-free interval would be necessary for tree recruitment.

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