J. For. 113(4):393–403
http://dx.doi.org/10.5849/jof.14-066

forest ecology

Impacts of Wildfire Recency and Frequency on an Appalachian Oak Forest

Melissa A. Thomas-Van Gundy, Katharina U. Wood, and James S. Rentch

Cabwaylingo State Forest in southern West Virginia has experienced numerous anthropogenic wildfires over the past 36 years. In this case study, we assessed the relationship between fire frequency and recency and stand composition and structure, with emphasis on oak and its competitors. Frequent and recent fire was significantly correlated with reduced red maple overstory stem density and basal area. Overstory oak density did not significantly vary with either fire frequency or recency. Total overstory basal area was greatest in areas of either no fire or nonrecent fire. Oak sapling density was significantly greater with high frequency and recent fire. Red maple sapling densities were greatest when fires were infrequent and recent, and red maple seedlings were greatest in no fire and low-frequency nonrecent fire areas. Our results suggest that recurring fire can enhance the development of large oak advanced reproduction. However, frequent fires without a sufficient fire-free interval could prevent the recruitment of oaks into the overstory.

Keywords: oak advanced reproduction, oak silviculture

Oak (*Quercus* spp.)-dominated forests have persisted for more than 6,000 years in the eastern United States (Webb 1988, Delcourt and Delcourt 1997). However, there is convincing evidence that these forests are shifting in species composition (Dyer 2006, Fei et al. 2011). This shift is particularly noticeable in the understory, where shade-tolerant species such as red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and blackgum (*Nyssa sylvatica* Marsh.) have generally increased in abundance (Steiner et al. 2008). On more mesic sites, oak advanced reproduction is less abundant and shade-intolerant, rapidly growing species such as yellow-poplar (*Liriodendron tulipfera* L.) and black cherry (*Prunus serotina* Ehrh) often outcompete oaks after timber harvest or other canopy disturbance (i.e., "recalcitrant oak accumulator systems" after Johnson et al. 2009). Successful oak advanced reproduction is now primarily confined to "intrinsic oak accumulator systems" (Johnson et al. 2009). These are drier, lower quality sites where understory light levels are greater and competitive pressure is less.

Attempts to explain this change in species composition have produced a lengthy list of the "usual suspects" (Lorimer 1993). Erratic seed production (Smith 1993), acorn herbivory (Johnson et al. 2009), deer browse (Rooney and Waller 2003), loss of American chestnut (*Castanea dentata* [Marsh.] Borkh.) and of passenger pigeons (*Ectopistes migratorius*) (Ellsworth and McComb 2003), shade from tall understory vegetation (Lorimer et al. 1994), and climate change (McEwan et al. 2011) have all been implicated. Researchers have also linked changing species composition with changes in natural disturbance patterns, particularly fire (Abrams 1992, Brose et al. 2001, Nowacki and Abrams 2008). According to this oak-fire hypothesis, oaks as a group are more adapted to and more likely to benefit from periodic fire than their competitors (Abrams 1992). After fire, germinating acorns benefit from a reduction in the litter layer and a reduction in populations of predatory insects and their habitat (Wright 1987, McCullough et al. 1998). Mature oaks have thick fire-resistant bark and can compartmentalize wounds caused by fire (Smith and Sutherland 1999). Oak species preferentially allocate carbohydrates to the root system, which enables seedlings to repeatedly resprout hypogeally after being top-killed if they receive sufficient light between fires. These seedling sprouts are more resistant to water stress because of higher conductive efficiency (Hodges and Gardiner 1992, Johnson et al. 2009).

Oak reproduction is often characterized as seedling sprout in origin with seedlings

Received June 20, 2014; accepted February 9, 2015; published online March 26, 2015.

Affiliations: *Melissa A. Thomas-Van Gundy (mthomasvangundy@fs.fed.us), USDA Forest Service, Northern Research Station, Parsons, WV. Katharina U. Wood (kumw66@gmail.com), affiliated with West Virginia University during the time of this work. James S. Rentch (jrentch2@wvu.edu), West Virginia University.*

Acknowledgments: *Eric Heitzman directed this research as part of a Master of Science thesis by K.U. Wood. Candice Butler assisted in fieldwork. We thank the staff at Cabwaylingo State Forest and Region 3, Milton Office of the West Virginia Division of Forestry, for their support. David McGill and four anonymous reviewers greatly improved the quality of this article. We thank the West Virginia Division of Forestry for financial support of K.U. Wood's MS work.*

undergoing dieback and resprouting (Johnson et al. 2009), although true seedlings are present, especially after abundant mast years. Fire, especially repeated fire, can affect seedling pools in several different ways, including reducing seedling density by top-killing thin-barked, fire-susceptible species and altering the seedbank (Schuler et al. 2010). Similarly, fires of sufficient intensity can reduce mid- and overstory tree density and thus increase light levels on the forest floor. By reducing the litter layer, fire may expose mineral soil and encourage germination and establishment of shade-intolerant species such as yellow-poplar and black birch (*Betula lenta* L.), which produce large numbers of small, wind-disseminated seed. Fire can also stimulate suckering of root-sprouting species such as sassafras (*Sassafras albidum* [Nutt.] Nees) (Griggs 1990). Finally, repeated fires can alter the seedling stratum by favoring oaks and hickories that readily sprout from dormant root collar buds located below the soil surface where they are insulated from injury (Hutchinson et al. 2005, Dey and Fan 2009).

A dramatic reduction in the frequency of fire in eastern oak forests over the past 80 years, due in part to fire control policies, has meant that many of the advantages provided by these adaptations are not realized. Nowacki and Abrams (2008) described this as the "mesophication" of eastern forests, a positive feedback cycle in which the removal of fire has resulted in a landscape that is increasingly fire-proof and less amenable to either the restoration of fire regimes or the maintenance of historically oak-dominated forests.

Although recognition of the importance of the role of fire in oak ecosystems has gained considerable traction, attempts to prove the oak-fire hypothesis using prescribed fire have produced mixed results. Many responses of oak regeneration to fire are found in the literature (for reviews, see Brose et al. 2006, 2013). Prescribed fire has been shown to increase the competitive status of oaks in some studies (Barnes and Van Lear 1998, Iverson et al. 2008, Brose 2010) and reduce it in others (Elliott and Vose 2010), whereas in still others the response was mixed (Collins and Carson 2003). An argument can be made that after 80 or more years of fire suppression, a single fire will probably not be sufficient to restore the full range of effects associated with the historic fire regime (Dey and Fan 2009). However, studies involving multiple prescribed fires in eastern oak forests have also reported mixed results with three or four fires reducing red maple seedling numbers but not improving the competitive position of oak seedlings (Alexander et al. 2008, Green et al. 2010), two or three fires reducing red maple saplings but also reducing oak sapling numbers and increasing red maple sprouts (Blankenship and Arthur 2006), and the composition of tree regeneration unchanged after two or four prescribed burns (Hutchinson et al. 2005). Whereas fire may be key to the development of a sufficient and competitive pool of oak advanced reproduction on mesic sites, the ultimate success may also depend on a fire-free period during which oak stems can grow beyond the sapling-size class (Guyette et al. 2006, Dey and Fan 2009, Arthur et al. 2012) and a reduction in canopy density to release oak advanced reproduction (Iverson et al. 2008, Hutchinson et al. 2012a, 2012b, Brose et al. 2013).

Studies on the impacts from multiple wildfires can also add to our knowledge of the role of fire in oak-dominated forests and its use as a management tool. A rare opportunity to investigate the impacts of multiple fires is found in Cabwaylingo State Forest (CSF) in southern West Virginia. The CSF is an oak-dominated forest that has experienced multiple anthropogenic wildfires over the past 36 years. Using a fire history map created for the forest, we sampled the area based on the number of fires experienced at a given location. The objective of this research was to document the impacts that fire frequency and recency have had on stand composition and structure. In this case study, any differences found between sample plots cannot be assumed to be only related to fire recency and frequency as we have no prefire data for any sample plots and have assumed that differences in prefire conditions were minimal. The initial size of any oak reproduction and competing vegetation is probably key to explaining species responses to fire (Brose et al. 2013); however, this is unknown for the study area. Also unknown are differences in fire severity and season. Even given the limitations of this case study of repeated fires over 36 years on the CSF, we believe important inferences of the impacts of repeated fires and the recency of fire can be made.

Methods

Study Area

CSF is located primarily in Wayne County, in southwestern West Virginia (Figure 1). The 8,150-acre state forest was established in 1933 from mostly old farmland and farm woodlots. The topography is highly dissected, consisting of rolling hills with 50% of the area being 25–40% slope, whereas slopes exceed 40% on another 33% of the area. The elevation in the study area varies from 938 ft to approximately 1,378 ft (West Virginia Division of Forestry [WVDOF] 2010).

The climate is hot continental (Bailey 1995). The average annual precipitation is 40 in. and is evenly distributed throughout the year. The average winter and summer temperatures are 33° F and 73° F, respectively. The frost-free season usually extends from the second week of April to the middle of October. Soils in the study area are primarily from the Dekalb-Pineville-Guyandotte association and are described as channery sandy loam (Dekalb) or channery loam (Pineville and Guyandotte) soils formed from weathered sandstone on moderately steep to very steep slopes and ridge tops, well-drained, with moderate productivity (Cole et al. 1999). The site index for northern red oak (*Quercus rubra* L.) ranges from 55 to 85 ft on this soil association (Cole et al. 1999).

Management and Policy Implications

The use of prescribed fire is increasing in oak-dominated forests, and in many areas multiple fires are considered necessary to meet restoration goals. Foresters and other land managers have questions on the number of fires needed, the timing of fires, and the effects of repeated burning on overstory and understory species composition and structure. A history of repeated wildfires on a state forest in West Virginia provided us a unique opportunity to investigate the impacts of multiple fires on oak-dominated forests. Our results show that frequent fires are correlated with significantly lower total basal area and greater abundance of oak saplings. These findings generally support the use of repeated prescribed fire as a management tool in oak forests; however, recency of fire, fire severity, and fire-free intervals must be considered. Other silvicultural practices such as herbicide and partial harvesting may also be needed in conjunction with repeated fires to further improve oak reproduction and restore oak-dominated forests.

(*Quercus velutina* Lam.), scarlet oak (*Quercus coccinea* Muenchh.), and chestnut oak (*Quercus prinus* L.) are usually abundant on the drier south and west aspects, upper slopes, and ridges. Red maple is omnipresent, comprising about 14% of the overstory trees and 8% of the basal area across all aspects and slope positions.

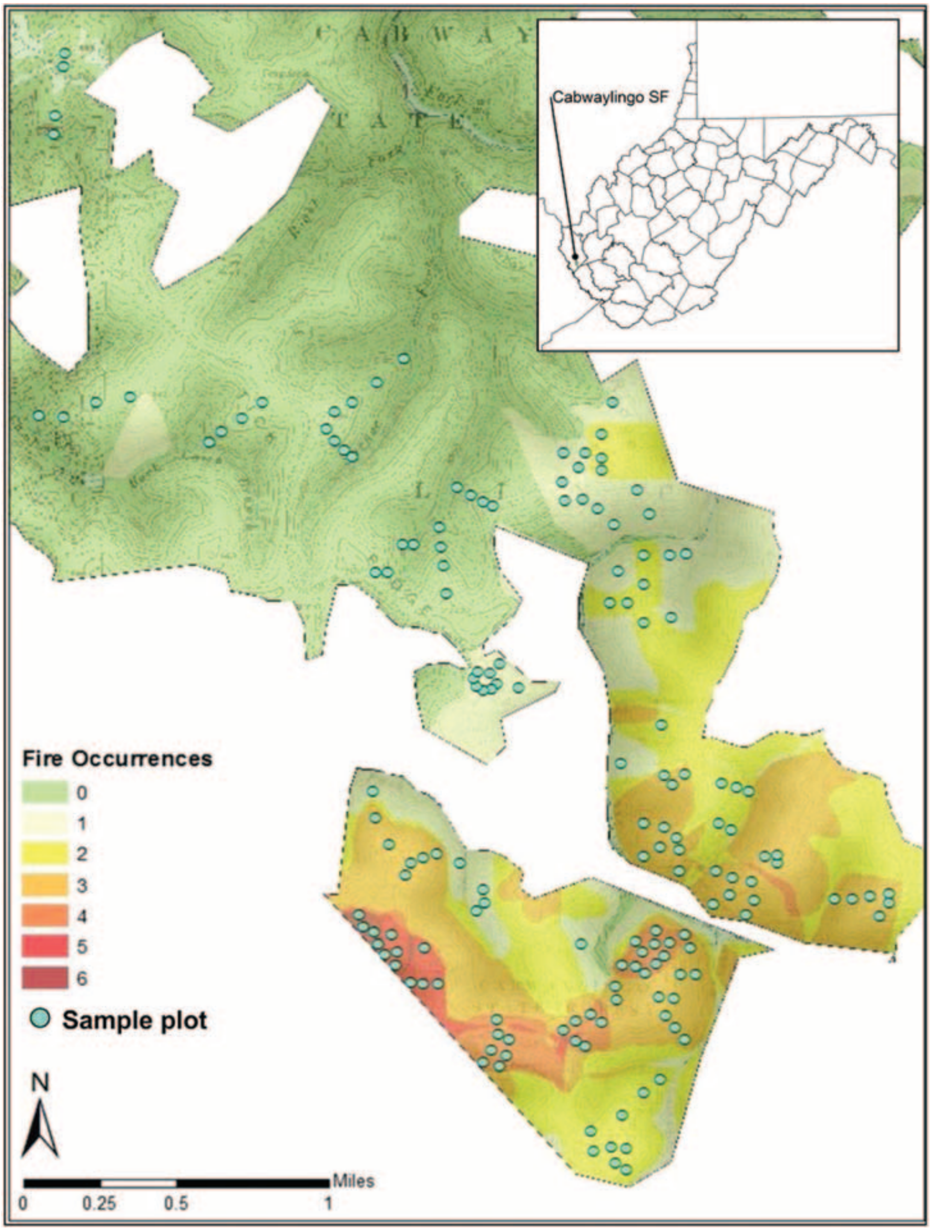

Figure 1. Location map, sample plots, and numbers of fires in the southern part of the CSF.

Fire Map Creation

To spatially describe the wildfires in the southern third of the CSF, we consulted fire reports of the WVDOF for the period 1972–2007. For fires greater than five acres, WVDOF reports included hand-drawn maps with major landmarks noted; fires after 2000 were mapped digitally by WVDOF and superposed onto topographic maps. Background and boundary features, along with point coordinates of probable ignition locations noted on the fire reports, were used to identify fire locations, which were then digitized in a geographic information system (GIS). All fires greater than 5 acres with spatial reference points were included in our digital fire map for a total of 43 fires.

Sample Point Locations

Sample points were located systematically so that all aspects, slope positions, and elevation ranges were represented. The number of fires ranged from 0 to 6 spanning years 1972 to 2007 (Figure 1). Given the unplanned nature of the wildfires, no attempt was made to establish the same number of sample points in each aspect, slope position, elevation range, or number of fires category. We limited sample points to areas of upland oak forest cover types, and plot centers were located at least 132 ft apart and outside of known timber harvest areas. In total, 164 sample locations in six different fire frequency areas were established (Figure 1; Table 1). As this is a case study of conditions postfire with no prefire data, we have made several assumptions. Given the history of the CSF, we assume that the forest is roughly even-aged, having developed from abandoned farmland, with some older forest patches that were farm woodlots. We also assumed that aspect influences the species composition and growth rates, given the ecological setting of the area (Fekedulegn et al. 2004), which is why all aspects were represented in the sampling.

In southern West Virginia, more than 99% of the fires are human-caused ignitions (Lynch and Hessl 2010). Most fires are surface fires of low severity occurring during the dormant season. Although wildfires have been suppressed by the WVDOF since the 1930s, in the past 36 years, parts of CSF have experienced many cultural fires associated with arson, debris burning, and moonshining; parts of the forest may have experienced a higher fire frequency than the historical range of variability. Although the fires in southern West Virginia may be low severity in general, fires on the CSF have been described by land managers on the CSF as setting parts of the forest back years in terms of developing to maturity (WVDOF 2010).

Because of past farming and uncontrolled fire before 1930, overstory forest composition is a mix of several types. The upland oak group (Eyre 1980) covers approximately 47% of the forest, with cove hardwoods making up about 34% and the maple-beech-hemlock type making up about 19% of the forest (WVDOF 2010). White oak (*Quercus alba* L.) is present over a range of sites from moist to dry. Northern red oak is more prevalent on moist sites, lower and middle slopes on north and east aspects, and coves and benches with deep and well-drained loamy soils. Black oak

Data Collection

Field data were collected between May and August of 2008. At each point, a plot center was established and three different types of plots were used to measure vegetation. First, a variable radius plot (basal area factor [BAF] = 20) was used to tally all living overstory trees ≥2 in. dbh by species and dbh. Second, one 1/100-acre sapling plot was established around the same prism plot center, and all saplings (stems ≥5 ft tall but <2 in. dbh) were recorded by species. Third, three milacre seedling plots were established 30 ft from the sapling plot center at azimuths of 0°, 120°, and 240° in which seedlings (stems <2 in. diameter at ground and <5 ft tall) were counted by species and height class. Height classes used were <1 ft, 1.0–1.5 ft, 1.6–2.5 ft, 2.6–3.5 ft, 3.6–4.5 ft, and >4.5 ft.

Table 1. Number sample plots by number of fires and recency of fire for the southern part of Cabwaylingo State Forest.

No. of fires over 36 years	No. of plots at years since last fire								
	0	3	7	9	13	23	27	28	Total
0	32	0	0	0	0	0	0	0	32
1	0*	0*	2*	0*	0†	4†	14†	11†	31
2	0*	0*	9*	0*	3†	0†	11†	0†	23
3	0*	10*	16*	7*	0†	0†	9†	0†	42
4	0‡	0‡	24‡	0‡	0	0	0	0	24
5 and 6	0‡	0‡	12‡	0‡	0	0	0	0	12
Total	32	10	63	7	3	4	34	11	164

* The 44 total plots categorized as low frequency and recent (LowF/Recent).
† The 52 plots categorized as low frequency and nonrecent (LowF/Nonrecent).
‡The 36 plots categorized as high frequency and recent (HighF/Recent).

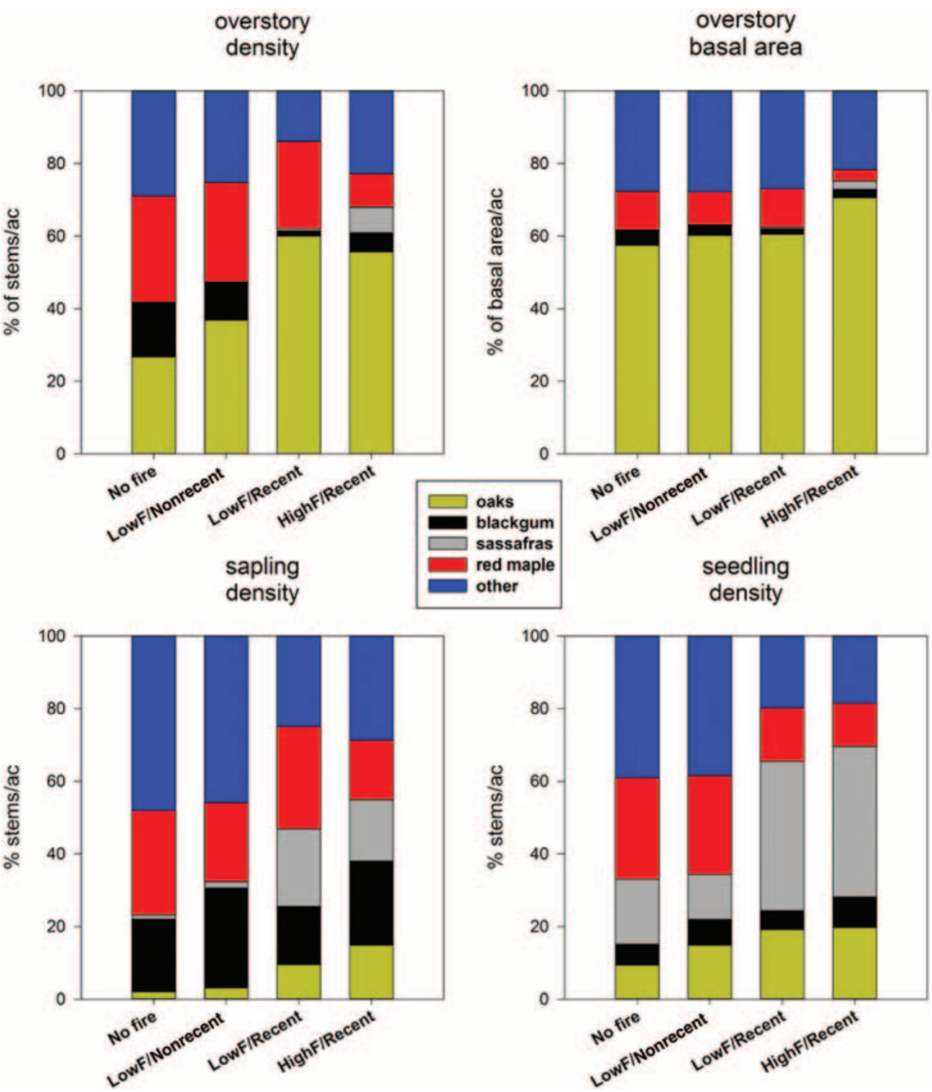

Figure 2. Species composition as a percentage of total for overstory (stems/acre and basal area/acre), saplings, and seedlings by frequency/recency category. The category "other" includes shagbark hickory, pignut hickory, bitternut hickory, white pine, Virginia pine, shortleaf pine, pitch pine, Florida dogwood, redbud, ironwood, sourwood, ash species, black walnut, basswood, and cucumber tree.

Data Analysis

Because wildfires were not synchronous across the 36-year time span of the data set, comparing sample plots only by number of fires seemed inappropriate and would only partially explain any differences found. For example, including data from plots having one fire 20 years ago with data from plots with one recent fire would ignore the role of time in the response of tree species to the disturbance. To include the elements of number of fires (frequency) and the time since last fire (recency), plots were categorized as either high or low frequency with either recent or nonrecent fire. High frequency was defined as 4 or more fires over 36 years and low frequency as 1–3 fires; recent fire was defined as any fire within the last 10 years and nonrecent fire as more than 10 years since the last fire. The 164 sample plots were categorized as high frequency and recent fire (HighF/Recent, 36 plots), low frequency and recent fire (LowF/Recent, 44 plots), low frequency and nonrecent fire (LowF/Nonrecent, 52 plots), or no fire in last 36 years (32 plots); there are no plots considered high frequency and nonrecent fire (Table 1). Time since the last fire was calculated from 2008 when data collection occurred. Given the unplanned nature of this study, it should be noted that the HighF/Recent sample plots come from the southern end of the CSF, whereas the other sample plot categories are more dispersed throughout the study area (Figure 1).

From the variable radius plots, we calculated basal area (ft^2/acre) and density (stems/acre) for trees >2 in. dbh for each sample plot. Sapling and seedling density (stems/acre) were also calculated for each sample plot from their respective fixed plots. Least-squares means were compared using the four fire recency and frequency categories to determine whether wildfire has resulted in differences in densities in the overstory, sapling, and seedling layers or in overstory basal area. Species or species groups considered included oak species, blackgum, sassafras, red maple, other nonoak species, and total species. Statistical inferences were made by least-squares means through a generalized linear mixed model (PROC GLIMMIX) (SAS Institute, Inc. 2013) with confidence intervals calculated through maximum likelihood estimation; significance was set at $\alpha = 0.05$. Degrees of freedom were calculated using the residual method with adjustments made for multiple comparisons through the Kramer-Tukey method. The data were modeled as either exponential or normal with log or identity link functions. Despite the known role of aspect in shaping species composition in the area (Fekedulegn et al. 2004), preliminary regression analyses showed little explanatory power in comparing sites grouped by aspect, elevation range, or slope position. All analyses were made using the four wildfire categories as the only explanatory variable.

Results

Species Composition

Descriptive measures of forest structure and species composition were developed from the plot data. Species composition of all strata on the CSF apparently has been affected by wildfire frequency and recency over the past 36 years (Figure 2). Although the overstory was dominated by oak species in all four fire categories (including no fire) based on basal area, only 26% of the stems were oak species in plots with no fire. The highest proportion oak density was 59% and found in LowF/Recent plots; however, the highest proportion of oak species basal area occurred on HighF/Recent plots at 70%. The occurrence of any fire, whether recent or nonrecent, doubled oak seedling density over that of areas with no fire. Recent fires were associated with increases in sassafras, particularly in the seedling stratum, with about double the number of seedlings compared with those for no fire or nonrecent fire (Figure 2).

In general, the proportion of red maple in most size classes declined with recent fire. In the overstory of HighF/Recent plots, only 9% of stems were red maple compared with 29% for plots with no fire, 27% for LowF/Nonrecent plots, and 24% on LowF/Recent plots. Only 3% of the basal area was in red maple in HighF/Recent plots, compared to 9 or 10% in the other fire categories. The percentage of red maple saplings was highest in no fire and LowF/Recent plots (28%) and lowest in HighF/Recent plots (16%). Recent fire affected red maple seedling relative abundance as well, with HighF/Recent plots with the lowest proportion at 12%, LowF/Recent plots with 15%, and LowF/Nonrecent and no fire plots with similar abundances at 27 and 28%, respectively (Figure 2).

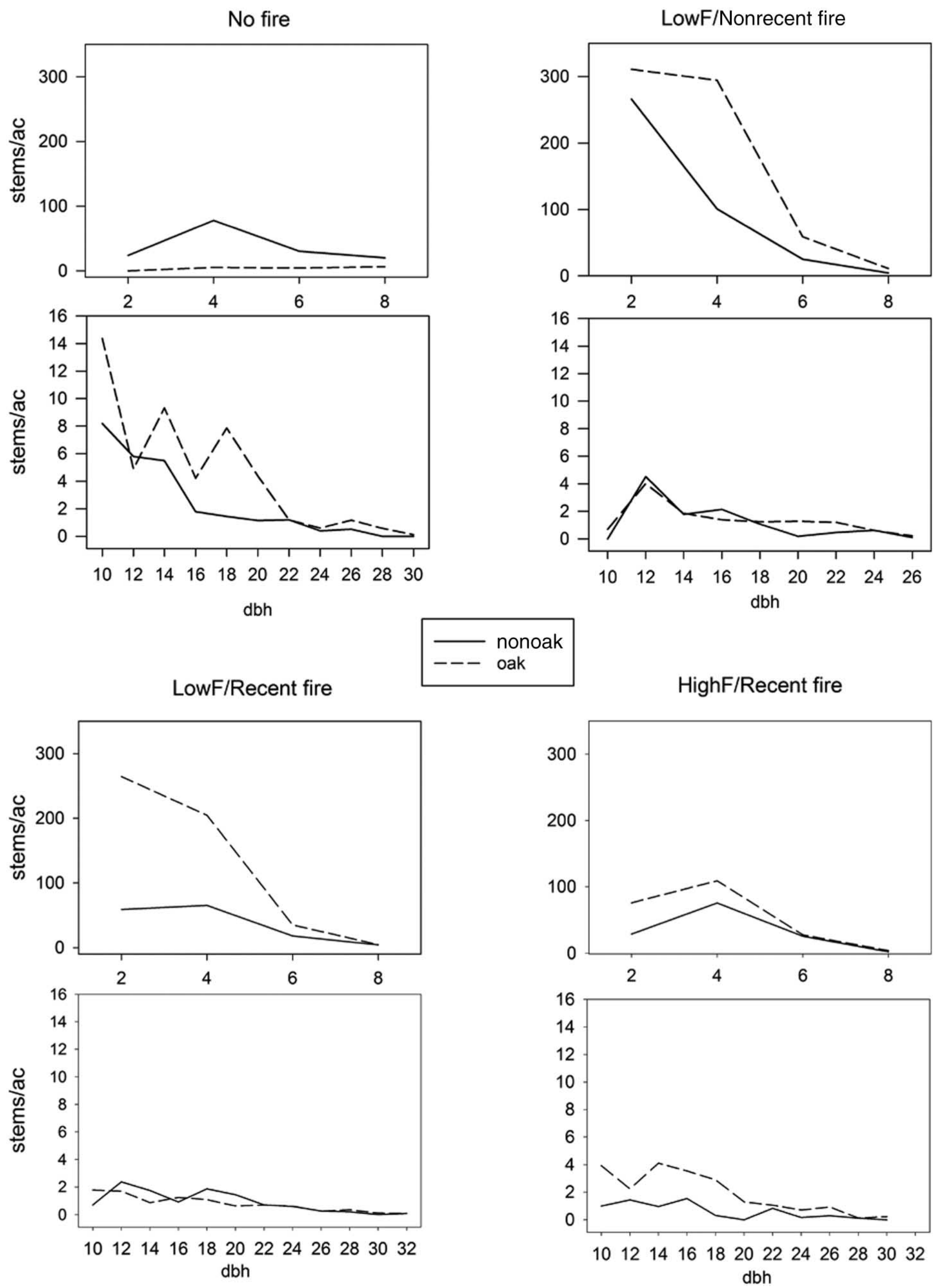

Figure 3. Stand structure by frequency/recency category. The distribution of stems/acre by 2 in. diameter dbh class is split for each fire category with the top graph depicting the distribution of stems 2–8 in. dbh and the lower graph depicting stems >10 in. dbh.

Stand Structure

Wildfires over the past 36 years appear to have affected the stand structure, displayed as the distribution of stems by 2-in. dbh class, on the CSF (Figure 3). In areas of low-frequency fire, there were greater numbers of small diameter stems (2–8 in. dbh) than for areas of no fire or HighF/Recent areas. It appears that fire of any frequency or recency class resulted in an increase in small diameter oaks over that of areas of no fire. However, areas in CSF with fires of any frequency or recency class displayed lower numbers of larger diameter (>10 in. dbh) overstory stems than areas with no fires in 36 years.

Overstory

The total overstory tree density in the CSF has been affected by frequent and recent fire with the HighF/Recent plots having the lowest total density (133 ± 26 [mean ± SE] stems/acre), although these plots were statistically different only from LowF/Nonrecent plots (251 ± 30 stems/acre) (Figure 4). Even though differences in the proportion of oaks by fire category were noted above (Figure 2) and the lowest mean density occurred on plots with no fires (65 ± 13 stems/acre), the average number of overstory oak did not differ significantly by any fire category (Figure 4). Average overstory red maple density was lowest on HighF/Recent plots (12 ± 7 stems/ac), with the density in these areas significantly less than those on the other fire categories. Other nonoak species in the overstory had lower densities on recent fire plots. Average stem densities on HighF/Recent and LowF/Recent plots were not different from each other, but differed significantly from no fire and LowF/Nonrecent plots. The density of sassafras in the overstory was greatest on HighF/Recent plots; however, given the high variability and low total numbers, the statistical model was a poor fit and significance between categories could not be determined.

The lowest total basal area occurred on HighF/Recent plots (72 ± 6 ft^2/acre), which was significantly lower than that on nonfire and LowF/Nonrecent plots but statistically the same as that on LowF/Recent plots (Figure 5). The mean basal area in oak species did not differ significantly by fire category (Figure 5). Although the lowest mean basal area for oak species was found on HighF/Recent plots (51 ± 6 ft^2/ac), oak species made up 70% of the basal area on HighF/Recent plots (Figure 2). The lowest mean red maple basal area was on HighF/Recent plots (2 ± 1 square ft^2/ac), and this was significantly less than the mean for the other three fire categories.

Saplings

In the sapling size class, oaks were most abundant when fires were frequent and recent (HighF/Recent). Oak sapling density was significantly greater on HighF/Recent plots: nearly 8 times greater than that on LowF/Nonrecent plots and 25 times greater than that on no fire plots (Figure 6). The lowest mean red maple densities were on nonfire plots, but statistically the densities in these areas were the same as the mean densities found on LowF/Nonrecent plots. Sassafras sapling densities appeared to respond to fire of either high or low frequency. The mean sapling density of all species appeared

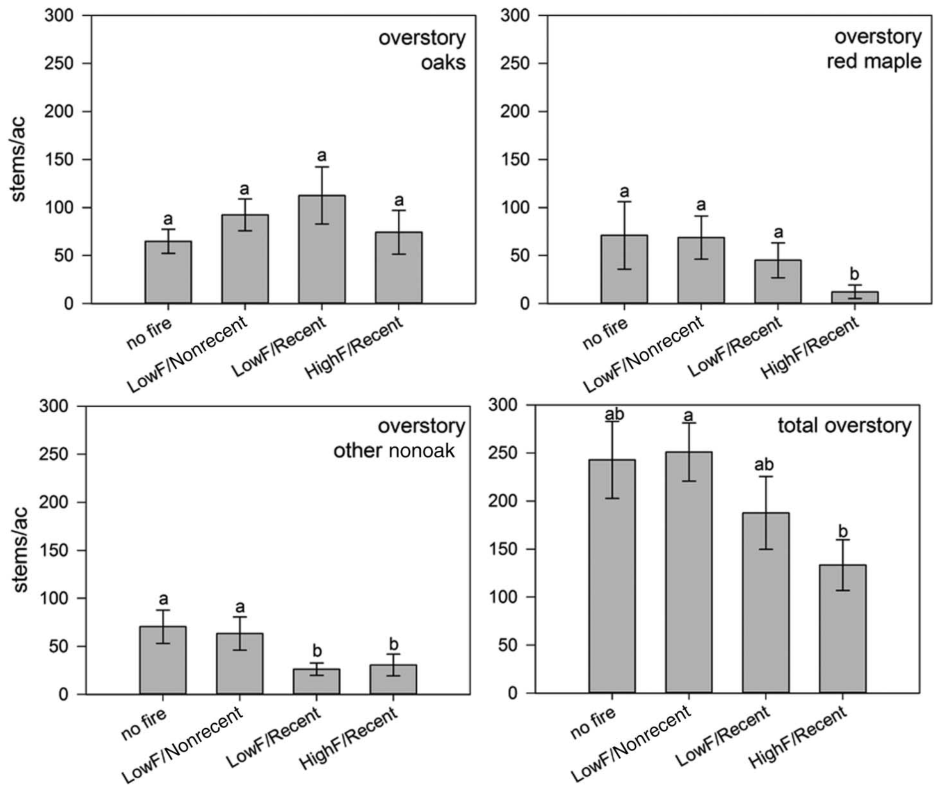

Figure 4. Mean density (stems/acre) and SE for selected species or genera and total species in the overstory by frequency/recency category. Means with the same letter are not significant (α = 0.05) based on generalized linear mixed-model analysis.

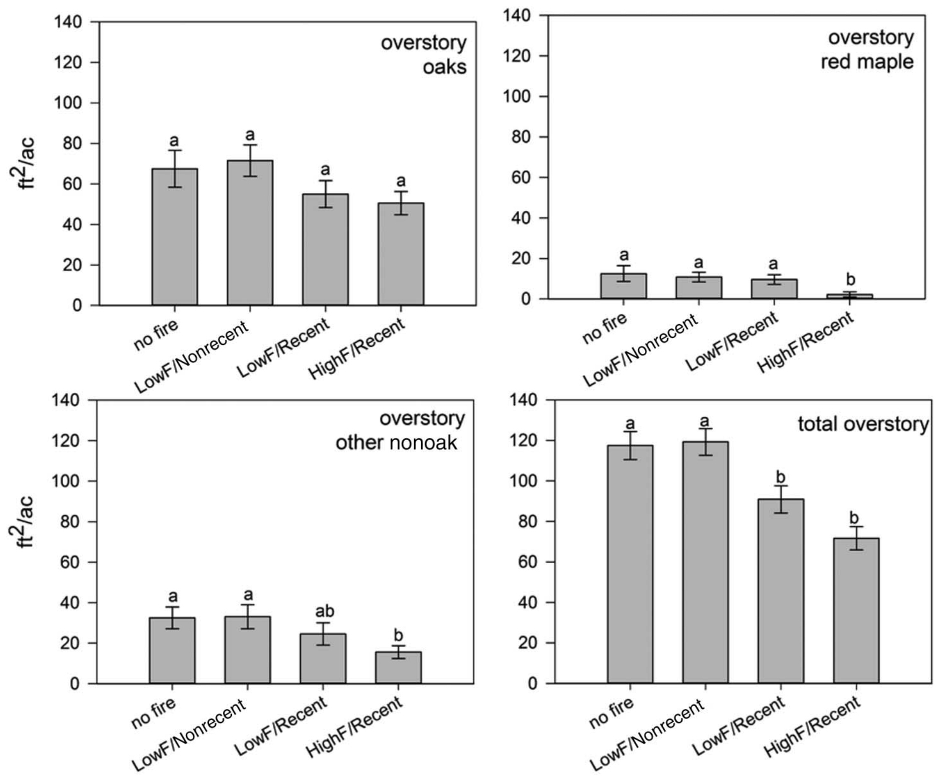

Figure 5. Mean basal area (ft^2/acre) and SE for selected species or genera and total species in the overstory by frequency/recency category. Means with the same letter are not significant (α = 0.05) based on generalized linear mixed-model analysis.

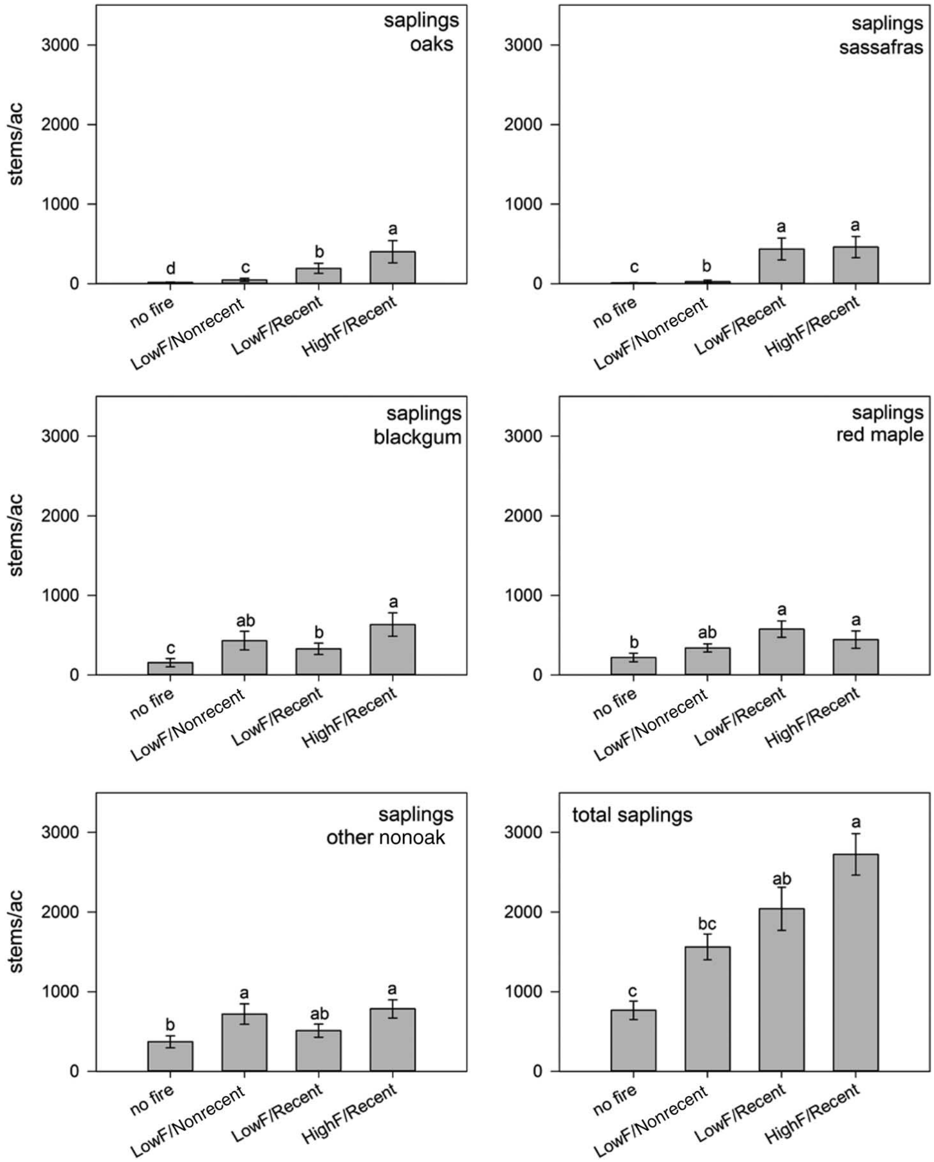

Figure 6. Mean density (stems/acre) and SE for selected sapling species or genera and total species by frequency/recency category. Means with the same letter are not significant (α = 0.05) based on generalized linear mixed-model analysis.

to be most closely linked to wildfire recency, with stem densities in both HighF/Recent and LowF/Recent plots significantly greater than those in plots with no fire.

Seedlings

Sites with recent fire had greater oak species seedling density relative to that of sites with no fire, but the means for HighF/Recent and LowF/Recent plots were statistically the same as the means for LowF/Nonrecent (Figure 7). Similarly, sassafras seedling density was greater in areas with recent fire. Densities of red maple and other nonoak species seedlings were also significantly lower on sites with recent fire. However, the variability of total mean seedling densities was very high, and total densities appeared to be unaffected by fire frequency or recency.

Because oak seedling height is a factor in regeneration success, the impacts of fire recency and frequency were explored by height class (Figure 8). For the smallest size class (<1 ft) the only significant difference in mean density was between no fire and LowF/Recent plots, with more oak stems on the LowF/recent plots. There were no differences between any plot types for oak seedlings 1.0–1.5 ft tall. LowF/Recent plots again showed the highest oak seedlings density for seedlings 1.6–2.5 ft tall; however, this was only statistically different from the mean for LowF/Nonrecent plots. For oak seedlings 2.6–3.5 and 3.6 to 4.5 ft tall, the pattern for mean density was the same, with HighF/Recent plots having significantly higher mean stem densities than the other plot types and mean densities on LowF/Nonrecent and LowF/Recent plots being statistically the same. The mean densities of oak seedlings 4.5 ft and larger were significantly greater on LowF/Recent and HighF/Recent plots than on LowF/Nonrecent and no fire plots; however, they were not significantly different from each other.

Discussion

Based on a growing appreciation of the historic role of fire in sustaining oak ecosystems, forest researchers have increasingly investigated the use of prescribed fire to enhance the oak regeneration potential of existing oak stands and to improve the competitive status of oak regeneration relative to its competitors (Brose et al. 2006, 2013). Although this study describes responses to wildfires rather than prescribed fires, it nevertheless quantifies the observed relationship of fire, especially repeated fires, on the structure and composition of an upland oak forest. The unburned sections of the CSF typify the current status of many eastern oak forests where oaks comprise 50% or more of total stocking, the mid- and understory are dominated by shade-tolerant species that cause low levels of sunlight at the forest floor, and the regeneration potential for oak is low. This situation represents the quintessential oak regeneration problem in the eastern United States and has been well documented throughout the region (Lorimer 1993, Nowacki and Abrams 2008, Johnson et al. 2009).

In this study, the apparent impact of wildfires on different forest strata varied, depending on species and both fire frequency and recency across environmental gradients in a second-growth oak-dominated forest. Other possible explanations for the differences found, such as differing initial conditions, variety in seedling sizes, and fire severity were untestable in this case study of postfire conditions. However, the density and basal area of thin-barked red maple were lower in the overstory in areas with frequent fire, and red maple seedlings were less abundant in areas with recent fire, as found in prescribed fire studies with controls (Schuler et al. 2013) and as would be expected based on fire ecology and the known response of

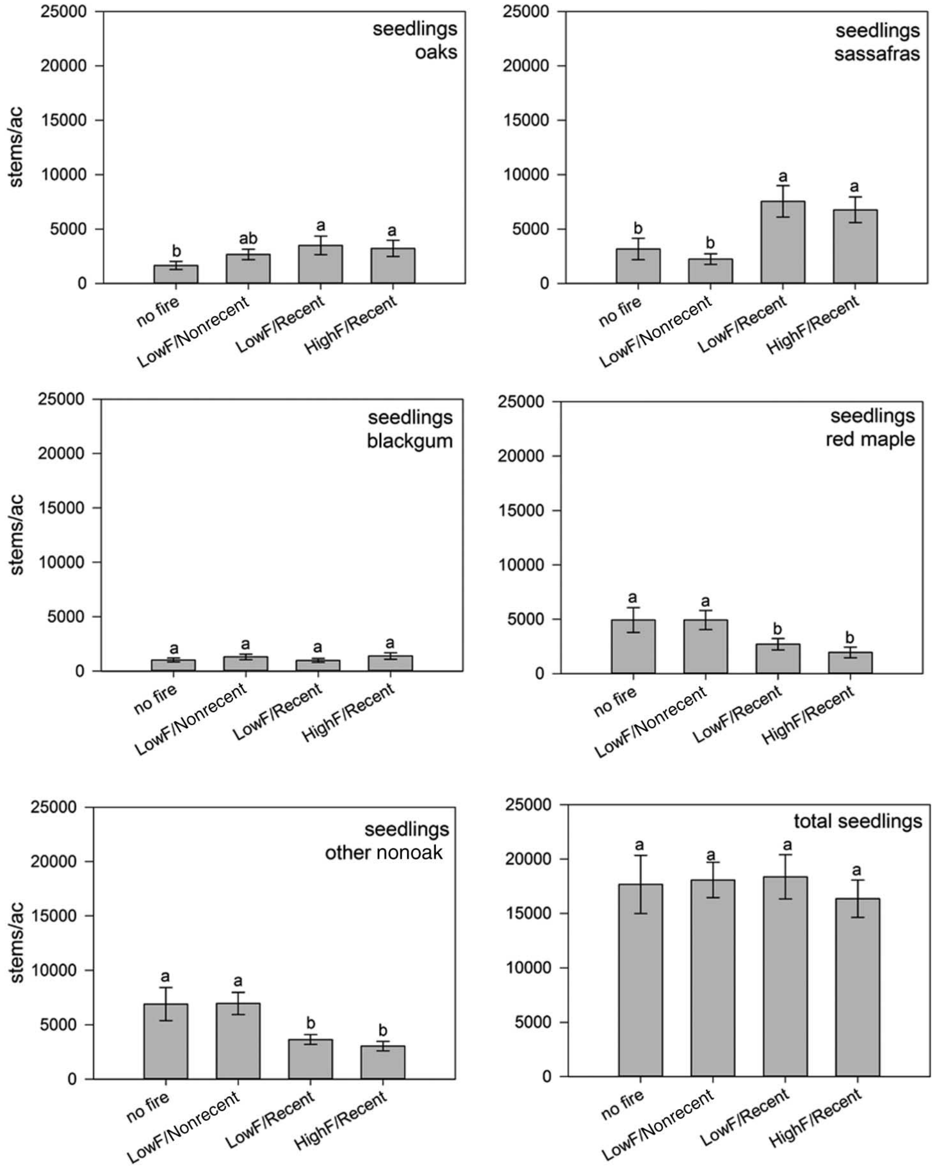

Figure 7. Mean density (stems/acre) and SE for selected seedling species or genera and total species by frequency/recency category. Means with the same letter are not significant (α = 0.05) based on generalized linear mixed-model analysis.

red maple to fire (Hare 1965, Harmon 1984, Bova and Dickinson 2005).

Overstory oaks appear to be largely unaffected by fire as would be expected given their fire-adapted traits such as thick, fire-resistant bark, and the ability to compartmentalize cambial damage and resist rot (Van Lear and Watt 1993, Smith and Sutherland 1999). Although oak species make up a relatively small portion of total sapling stocking, oak saplings were more abundant in plots with four or more wildfires in 36 years. However, even sites with infrequent fires yielded significantly greater oak sapling density than no fire sites. Taller oak seedlings appeared to be correlated with recency of fires (within the last 10 years) regardless of frequency.

On the CSF, sapling density was generally greater on plots with higher fire frequency, with higher numbers of competitors of oak such as blackgum, sassafras, and black locust (*Robinia pseudoacacia* L.) compared with those on no fire or low-frequency plots. These species are often associated with early successional stands created by large disturbances, and the HighF/Recent and LowF/Recent plots had lower total basal area than the no fire and LowF/Nonrecent plots, indicating possible changes in available light sometime in the past. Oak sapling density on the HighF/Recent plots was double that of LowF/Recent plots, 8 times the density of LowF/Nonrecent plots, and 25 times the density of nonfire plots. Our findings support recent studies and reviews highlighting the need for canopy reduction in conjunction with prescribed fire for successful oak regeneration (Iverson et al. 2008, Hutchinson et al. 2012a, 2012b, Brose et al. 2013).

In a postwildfire study of oak forests in the Ridge and Valley province of Pennsylvania, Signell et al. (2005) found little sapling regeneration of any species in unburned stands and abundant oak saplings in burned stands. The oak saplings in the burned stands appeared to be associated with areas of lower canopy and subcanopy tree density in their study area (Signell et al. 2005). Regression analysis showed a significant relationship between overstory density and oak sapling presence, with oak saplings virtually absent at more than 162 stems/acre. Similarly on the CSF, mean total overstory density in the HighF/Recent plots was approximately 133 stems/acre. However, unlike the Pennsylvania forests, our plots with high numbers of oak saplings were also not those with low total sapling densities. Our methods for determining fire history differ from those used in the Pennsylvania study; Signell et al. (2005) used dendrochronology to determine the number of major fires in the study stands since stand establishment. Stands with repeated fires in the Pennsylvania study experienced at most 4 major fires in about 70 years (Signell et al. 2005). The use of fire scars in tree cores may have missed some lower intensity fires that would have been recorded if fire records similar to ours were available. However, even given the differences in fire history and methods, the relationship between oak sapling numbers and lower overstory densities is similar.

Although frequent fire appears to be associated with increased oak sapling density, more than four fires over 36 years may create a problem for the survival of oak saplings. Using the same data set as assessed here, Wood (2010) found that oak sapling density decreased from 571 stems/acre after 4 fires to just 67 stems/acre with 5 or 6 fires. These individuals may persist in the stands as seedling sprouts and may regain sapling status given time. However, the plots with five or six fires share the same most recent fire (2001) with the plots having four fires; differences in initial conditions, differences in fire severity, or the additional fires in the past

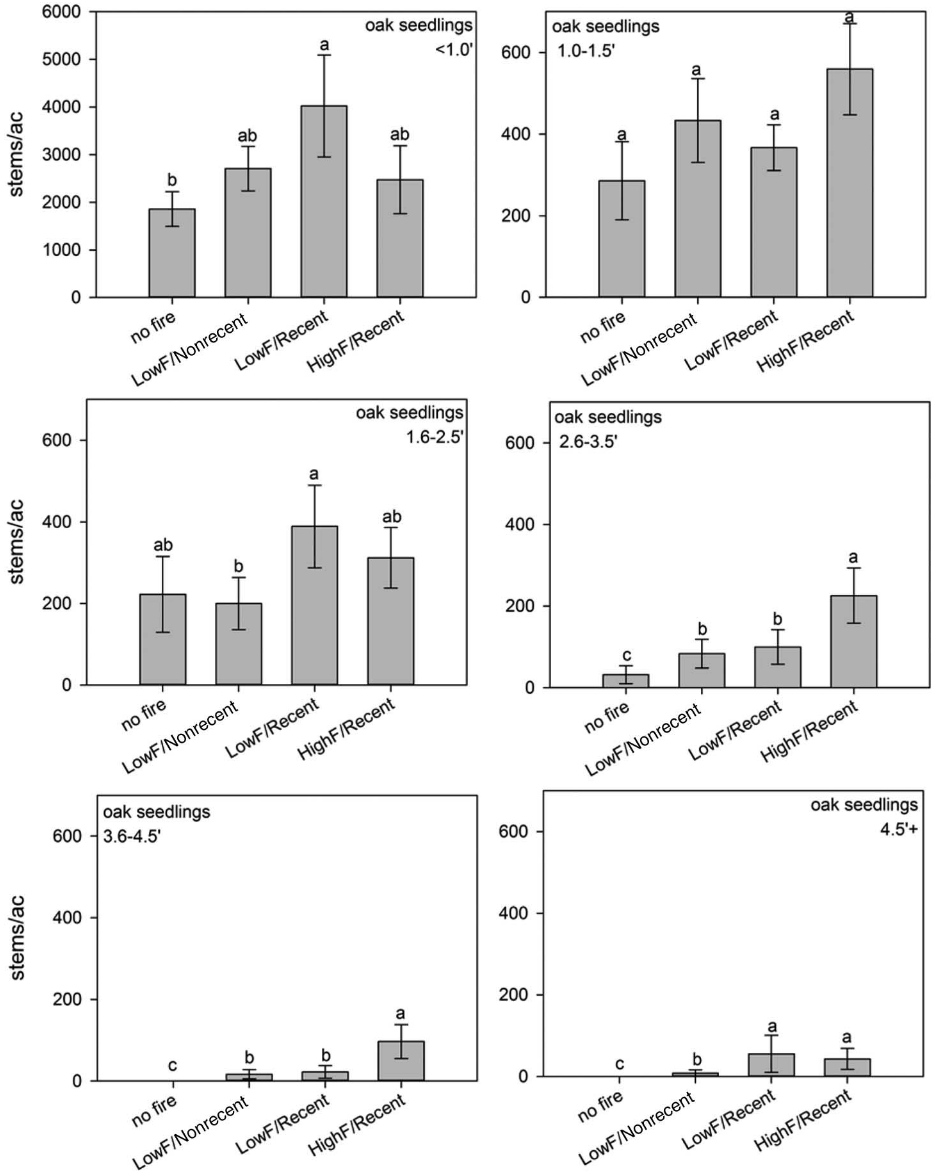

Figure 8. Mean density (stems/acre) and SE for oak seedlings by height class and frequency/recency category. Means with the same letter are not significant (α = 0.05) based on generalized linear mixed-model analysis.

created the differences seen in oak saplings between these plots. There seems to exist a window in which fire frequency is "just enough but not too much" in the oak regeneration process. Recognition of this nonlinearity deepens our appreciation of the complexity of the oak-fire relationship. Whereas repeated fire may enhance oak regeneration potential, it can also reduce it if surviving oak stems do not have a sufficiently long fire-free interval to grow past the sapling size class and recruit into the overstory (Dey and Fan 2009, Burton et al. 2010, Fan et al. 2012).

Estimates of the needed length of the fire-free interval vary with site characteristics, previous fire intensity, the level of competition, and overstory structure (Brose 2004, Arthur et al. 2012); however, little research has been conducted on this question. Based on oak site index curves (Carmean et al. 1989), upland oaks require 12–30 years for a sapling-size stem to reach a height of 30 ft, roughly the lower level of the overstory, depending on site quality. This time estimate is consistent with the historical record of wildfires in this region. Although Shumway et al. (2001) found a median fire interval of 7.6 years in an old-growth mixed-oak stand in western Maryland, fire-free intervals of 10–25 years were fairly common. McEwan et al. (2007) found an irregular temporal pattern of fires in southeastern Ohio and Kentucky for the years 1875–1940; among sites, there were large differences between minimum and maximum fire return intervals, and most of the stands had periods of frequent fire followed by periods when fire was absent. This temporal pattern may be necessary to allow surviving oak seedlings and saplings sufficient time to ascend to the overstory.

Finally, it is important to note that many of these wildfires are of unknown origins, and we have no measure of fire severity or the extent of tree mortality associated with any individual fire. As part of a companion study, we did estimate total char height of fire scars on trees, but this was a cumulative estimate, not an indication of the intensity of any single fire. In addition, the study was not designed to analyze fire impacts based on season of burning. This may be an important factor since the sprouting capacity of top-killed oak seedlings after growing-season burns has been shown to be greater than that of their competitors due to the greater investment of oaks in root biomass (Brose and Van Lear 1998). The stand structure data (Figure 3) suggest that there may have been high severity fires in the past 36 years. This complicates the use of results from wildfires in the design of management actions especially if prescribed fire is constrained to low intensity.

Conclusion

Whereas the fire history of the CSF represents a unique and unplanned experiment, the study area is representative of many oak-dominated second-growth forests, and the findings from this case study provide important information on fire effects on oak regeneration. Four or more fires in 36 years resulted in greater numbers of oak saplings than in areas of low-frequency fires (either recent or nonrecent) and no fire areas. To develop management guidelines for using prescribed fire to establish successful oak regeneration, it may not be enough to simply "average out" a certain number of burns over a defined period of time. The most recent fire in the plots on the CSF where the greatest number of oak saplings were found was in 2001, 7 years before the data used for analysis were collected, supporting the findings of others of the need for a fire-free period to allow for oak sapling development and recruitment (Brose 2004, Johnson et al. 2009, Dey et al. 2010, Brose et al. 2014).

Literature Cited

ABRAMS, M.D. 1992. Fire and the development of oak forests. *BioScience* 42(5):346–353.

ALEXANDER, H.D., M.A. ARTHUR, D.L. LOFTIS, AND S.R. GREEN. 2008. Survival and growth of upland oak and co-occurring competitor seedlings following single and repeated prescribed fires. *For. Ecol. Manage.* 256:1021–1030.

ARTHUR, M.A., H.D. ALEXANDER, D.C. DEY, C.J. SCHWEITZER, AND D.L. LOFTIS. 2012. Refining the oak-fire hypothesis for management of oak-dominated forests of the eastern United States. *J. For.* 110:257–266.

BAILEY, R.G. 1995. *Description of the ecoregions of the United States*, 2nd ed. USDA For. Serv., Misc. Publ. 1391, Washington, DC. 126 p.

BARNES, T.A., AND D.H. VAN LEAR. 1998. Prescribed fire effects on advanced regeneration in mixed hardwood stands. *South. J. Appl. For.* 22:138–142.

BLANKENSHIP, B.A., AND M.A. ARTHUR. 2006. Stand structure over nine years in burned and fire- excluded oak stands on the Cumberland Plateau, Kentucky. *For. Ecol. Manage.* 225: 134–145.

BOVA, A.S., AND M.S. DICKINSON. 2005. Linking surface-fire behavior, stem heating, and tissue necrosis. *Can. J. For. Res.* 35:814–822.

BROSE, P.H. 2004. Fitting fire into oak management. P. 263 in *Upland oak ecology symposium: History, current conditions, and sustainability*, Spetich, M.A. (ed.). USDA For. Serv., Gen. Tech. Rep. SRS-73, Southern Research Station, Asheville, NC.

BROSE, P.H. 2010. Long-term effects of single prescribed fires on hardwood regeneration in oak shelterwood stands. *For. Ecol. Manage.* 260(9):1516–1524.

BROSE, P.H., AND D.H. VAN LEAR. 1998. Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. *Can. J. For. Res.* 28:331–339.

BROSE, P., T. SCHULER, D. VAN LEAR, AND J. BERST. 2001. Bringing fire back: The changing regimes of the Appalachian mixed-oak forest. *J. For.* 99:30–35.

BROSE, P., T. SCHULER, AND J. WARD. 2006. Responses of oak and other hardwood regeneration to prescribed fire: What we know as of 2005. P. 123–135 in *Fire in eastern oak forests: Delivering science to land managers, proc. of a conference; 2005 November 15–17, Columbus, OH,* Dickinson, M.B. (ed.). USDA For. Serv., Gen. Tech. Rep. NRS-P-1, Northern Research Station, Newtown Square, PA.

BROSE, P.H., D.C. DEY, R.J. PHILLIPS, AND T.A. WALDROP. 2013. A meta-analysis of the fire-oak hypothesis: Does prescribed burning promote oak reproduction in eastern North America? *For. Sci.* 59(3):322–334.

BROSE, P.H., D.C. DEY, AND T.A. WALDROP. 2014. *The fire-oak literature of eastern North America: Synthesis and guidelines.* USDA For. Serv., Gen. Tech. Rep. NRS-135, Northern Research Station, Newtown Square, PA. 98 p.

BURTON, J.A., S.W. HALLGREN, AND M.W. PALMER. 2010. Fire frequency affects structure and composition of xeric forests of eastern Oklahoma. *Nat. Areas J.* 30(4):370–379.

CARMEAN, W.H., J.T. HAHN, AND R.D. JACOBS. 1989. *Site index curves for forest tree species in the eastern United States*. USDA For. Serv., Gen. Tech. Rep. NC-128, North Central Forest Experiment Station, St. Paul, MN.

COLE, C.P., E.N. THOMPSON, D.A. ADAMO, P.D. DIXON, R.J. FUGILL, AND S.L. HOOVER. 1999. *Soil survey of Wayne County, West Virginia*. USDA Natural Resources Conservation Service, Washington, DC. 150 p.

COLLINS, R.J., AND W.P. CARSON. 2003. The fire and oak hypothesis: Incorporating the influence of deer browsing and canopy gaps. P. 44–45 in *Proc. of the 13th Central hardwood forest conference*, Van Sambeek, J.W., J.O. Dawson, F. Ponder Jr., E.F. Lowenstein, and J.S. Fralish (eds.).USDA For. Serv., Gen. Tech. Rep. NC-234, North Central Forest Experiment Station, St. Paul, MN.

DELCOURT, H.R., AND P.A. DELCOURT. 1997. Pre-Columbian Native American use of fire on southern Appalachian landscapes. *Conserv. Biol.* 11:1010–1014.

DEY, D.C., A.A. ROYO, P.H. BROSE, T.F. HUTCHINSON, M.A. SPECTICH, AND S.H. STOLESON. 2010. An ecologically based approach to oak silviculture: A synthesis of 50 years of oak ecosystem research in North America. *Rev. Col. For.* 13(2):200–222.

DEY, D.C., AND Z. FAN. 2009. A review of fire and oak regeneration and overstory recruitment. P. 2–20 in *Proc. of the 3rd Fire in eastern oak forests conference*, Hutchinson, T.F. (ed.). USDA For. Serv., Gen. Tech. Rep. NRS-46, Northern Research Station, Newtown Square, PA.

DYER, J.M. 2006. Revisiting the deciduous forests of eastern North America. *BioScience* 56: 341–352.

ELLIOTT, K.J., AND J.M. VOSE. 2010. Short-term effects of prescribed fire on mixed oak forests in the southern Appalachians: Vegetation response. *J. Torr. Bot. Soc.* 137:49–66.

ELLSWORTH, J.W., AND B.C. MCCOMB. 2003. Potential effects of passenger pigeon flocks on the structure and composition of presettlement forests of eastern North America. *Conserv. Biol.* 17:1548–1558.

EYRE, F.H. (ED.). 1980. *Forest cover types of the United States and Canada*. Society of American Foresters, Washington, DC. 148 p.

FAN, Z., Z. MA, D.C. DEY, AND S.D. ROBERTS. 2012. Response of advance reproduction of oaks and associated species to repeated prescribed fires in upland oak-hickory forests, Missouri. *For. Ecol. Manage.* 266:160–169.

FEI, S., N. KONG, K.C. STEINER, W.K. MOSER, AND E. STEINER. 2011. Change in oak abundance in the eastern United States from 1980 to 2008. *For. Ecol. Manage.* 262:1370–1377.

FEKEDULEGN, D., J.J. COLBERT, J.S. RENTCH, AND K.W. GOTTSCHALK. 2004. Aspect induced differences in vegetation, soil, and microclimatic characteristics of an Appalachian watershed. *Castanea* 69(2):92–108.

GREEN, S.R., M.A. ARTHUR, AND B.A. BLANKENSHIP. 2010. Oak and red maple seedling survival and growth following periodic prescribed fire on xeric ridgetops on the Cumberland Plateau. *For. Ecol. Manage.* 259:2256–2266.

GRIGGS, M.M. 1990. *Sassafras albidum* (Nutt.) Nees sassafras. P. 773–777 in *Silvics of North America, Vol. 2: Hardwoods*, Burns, R.M., and B.H. Honkala (tech. cords.). USDA For. Serv., Agri. Handbk. 654, Washington, DC.

GUYETTE, R.P., M.A. SPETICH, AND M.C. STAMBAUGH. 2006. Historic fire regime dynamics and forcing factors in the Boston Mountains, Arkansas. *For. Ecol. Manage.* 234:293–304.

HARMON, M.E. 1984. Survival of trees after low-intensity surface fires in Great Smoky Mountains National Park. *Ecology* 65(3):796–802.

HARE, R.C. 1965. Contribution of bark to fire resistance. *J. For.* 63(4):248–251.

HODGES, J.D., AND E.S. GARDINER. 1992. Ecology and physiology of oak regeneration. P. 54–65 in *Oak regeneration: Serious problems, practical recommendations (symposium proceedings)*, Loftis, D.L., and C.E. McGee (eds.). USDA For. Serv., Gen. Tech. Rep. SE-84, Southeastern Research Station, Asheville, NC.

HUTCHINSON, T.F., E.K. SUTHERLAND, AND D.A. YAUSSEY. 2005. Effects of repeated prescribed fires on the structure, composition, and regeneration of mixed-oak forests in Ohio. *For. Ecol. Manage.* 218:210–228.

HUTCHINSON, T.F., R.P. LONG, J. REBBECK, E.K. SUTHERLAND, AND D.A. YAUSSY. 2012a. Repeated prescribed fires alter gap-phase regeneration in mixed-oak forests. *Can. J. For. Res.* 42:303–314.

HUTCHINSON, T.F., D.A. YAUSSY, R.P. LONG, J. REBBECK, AND E.K. SUTHERLAND. 2012b. Long-term (13-year) effects of repeated prescribed fires on stand structure and tree regeneration in mixed-oak forests. *For. Ecol. Manage.* 286:87–100.

IVERSON, L.R., T.F. HUTCHINSON, A.M. PRASAD, AND M.P. PETERS. 2008. Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern US: 7-year results. *For. Ecol. Manage.* 255:3035–3050.

JOHNSON, P.S., S.R. SHIFLEY, AND R. ROGERS. 2009. *The ecology and silviculture of oaks,* 2nd ed. CABI Publishing, Cambridge, MA. 580 p.

LORIMER, C.G. 1993. Causes of the oak regeneration problem. P. 14–39 in *Oak regeneration: Serious problems, practical recommendations*, Loftis, D.L., and C.E. McGee (eds.). USDA For. Serv., Gen. Tech. Rep. SE-84, Southeastern Research Station, Asheville, NC.

LORIMER, C.G., J.W. CHAPMAN, AND W.D. LAMBERT. 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. *J. Ecol.* 82:227–237.

LYNCH, C., AND A. HESSL. 2010. Climatic controls on historical wildfires in West Virginia, 1939–2008. *Phys. Geog.* 31:254–269.

MCCULLOUGH, D.G., R.A. WERNER, AND D. NEUMANN. 1998. Fire and insects in northern and boreal forest ecosystems of North America. *Annu. Rev. Entomol.* 43:107–127.

MCEWAN, R.W., T.F. HUTCHINSON, R.P. LONG, R.D. FORD, AND B.C. MCCARTHY. 2007. Temporal and spatial patterns in fire occurrence during the establishment of mix-oak forests in eastern North American. *J. Veg. Sci.* 18: 655–664.

McEwan, R.W., J.M. Dyer, and N. Pederson. 2011. Multiple interacting ecosystem drivers: Toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography* 34:244–256.

Nowacki, G.J., and M.D. Abrams. 2008. The demise of fire and "mesophication" of forest in the eastern United States. *BioScience* 58:123–138.

Rooney, T.P., and D.M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *For. Ecol. Manage.* 181:165–176.

SAS Institute, Inc. 2013. *SAS enterprise guide 6.1.* SAS Institute, Inc., Cary, NC.

Schuler, T.M., M. Thomas-Van Gundy, M.B. Adams, and W.M. Ford. 2010. *Seed bank response to prescribed fire in the central Appalachians*. USDA For. Serv., Res. Pap. NRS-9, Northern Research Station, Newtown Square, PA.

Schuler, T.M., M. Thomas-Van Gundy, M.B. Adams, and W.M. Ford. 2013. Analysis of two pre-shelterwood prescribed fires in a mesic mixed-oak forest in West Virginia. P. 430–446 in *Proc. of the 18th central hardwood forest conference, 2012 March 26–28, Morgantown, WV*, Miller, G.W., T.M. Schuler, K.W. Gottschalk, J.R. Brooks, S.T. Grushecky, B.D. Spong, and J.S. Rentch (eds.). USDA For. Serv., Gen. Tech. Rep. NRS-P-117, Northern Research Station, Newtown Square, PA.

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

Smith, D.W. 1993. Oak regeneration: The scope of the problem. P. 40–52 in *Oak regeneration: Serious problems, practical recommendations*, Loftis, D.L., and C.E. McGee (eds.). USDA For. Serv., Gen. Tech. Rep. SE-84, Southeastern Research Station, Asheville, NC.

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

Steiner, K.C., J.C. Finley, P.J. Gould, S. Fei, and M. McDill. 2008. Oak regeneration guidelines for the central Appalachians. *North. J. Appl. For.* 25:5–16.

Van Lear, D.H., and J.M. Watt. 1993. The role of fire in oak regeneration. P. 40–52 in *Oak regeneration: Serious problems, practical recommendations*, Loftis, D.L., and C.E. McGee (eds.). USDA For. Serv., Gen. Tech. Rep. SE-84, Southeastern Research Station, Asheville, NC.

Webb, T. III. 1988. Eastern North America. P. 385–413 in *Vegetation history*, Huntley, B., and T. Webb III (eds.). Kluwer Academic Publishers, Boston, MA.

West Virginia Division of Forestry. 2010. *Cabwaylingo State Forest, forest resources management plan*. Available online at www.wvforestry.com/cabwaylingostateforest.cfm; last accessed Feb. 1, 2013.

Wood, K.U.M. 2010. *Ecological and economic impacts of wildfires on an Appalachian oak forest in southern West Virginia*. MSc thesis, Davis College of Agriculture, Forestry, & Consumer Science, West Virginia University, Morgantown, WV. 45 p.

Wright, S.L. 1987. *Managing insects affecting oak regeneration by prescribed burning*. USDA For. Serv., Gen. Tech. Rep. SE-46, Southeastern Forest Experiment Station, Asheville, NC.