

Research paper

Effects of burn season on large seedlings of oak and other hardwood regeneration three years after shelterwood harvest

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Abstract. The effects of fall and spring prescribed fires on large seedlings (0.3 to 1.3 m height) of oak and other hardwood species three years after a shelterwood harvest were examined in Richland Furnace and Zaleski State Forests in southern Ohio. Fall and spring burns appeared to be more deleterious to red oaks (*Quercus rubra* L., *Q. velutina* Lam., *Q. coccinea* Muenchh.) than white oaks (*Q. alba* L., *Q. prinus* L.). Red oak experienced reductions in numbers and canopy volume after spring burns, and canopy reductions after fall burns. White oak experienced small increases in numbers of stems after both fall and spring burns, and an increase in the canopy volume after fall burns, but a slight decrease after spring burns. Yellow-poplar (*Liriodendron tulipifera* L.), a major oak competitor prior to fire, experienced dramatic reductions in the number of regenerating stems and canopy volume after both fall and spring burns. On the other hand, red maple (*Acer rubrum* L.) experienced large increases in the number of regenerating stems and canopy volume after both fall and spring burns. Based on importance value, the oak species remained relatively unchanged after both fall and spring burns. Yellow-poplar became the least dominant species after spring burns and the second to last dominant species after fall burns.

Key words: prescribed fire, burn season, seedling, regeneration, shelterwood harvest.

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Introduction

Throughout the history of eastern North America, oak (*Quercus* spp.) has dominated many of the forests and woodlands (Delcourt & Delcourt, 1987; McShea & Healy, 2002). However, regenerating oak stands, particularly on productive sites, have been

an important problem for resource managers (Lorimer *et al.*, 1994; Brose *et al.*, 1999). It is difficult to get and keep the oak in a dominant position in the forest partly due to the species' slow growth and shade intolerance. Oak's capacity to regenerate itself is limited, especially in high-density forests. Without any type of disturbance

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that would reduce the amount of forest canopy, oak succumbs to more shade-tol-erant species, such as red maple (*Acer ru-brum* L.), American beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.). Shade-tolerant species therefore become well-established in the midstory and understory in the absence of disturbance, slowly replacing and dominating oaks in the overstory (Abrams & Downs, 1990). This problem has been exacerbated by fire exclusion policies in the U.S. over many decades in the past (Abrams, 1992; Lorimer, 1993; Van Lear & Brose, 2002).

Fire within ecosystem communities often creates opportunities for seed germination and seedling establishment (Glasgow & Matlack, 2007), especially in fire-dependent communities such as oak forests. Prescribed fire has been used to regenerate oak-dominated stands and improve the sustainability of oak forests (McShea & Healy, 2002). Fire can increase the regeneration potential of oak through three different mechanisms: (1) reduce the tree shade by opening up the canopy, which allows shade-intolerant oak to develop the size and mass of their root system; (2) control competition from more fire-sensitive species in the understory (Hutchinson et al., 2005); and (3) improve more favorable microsite conditions for germination and seedling establishment (Hoffmann, 1996; D'Antonio et al., 2001).

Because red maple, yellow poplar (*Liriodendron tulipifera* L.) and oak occupy many sites together in the reproduction layer, competition exists among them. When oak exists with its competitors, which often are higher numbers of shade-tolerant (fire-sensitive) trees, it displays slow growth (Steinhoff, 1978). Shade-tolerant species can make significant height growth and increase both in number and size steadily under a closed canopy, and thus have an important advantage over oaks (Loftis & McGee, 1993).

The composition of a fire-prone ecosystem is influenced by fire frequency, intensi-

ty and the time of year, or season, when fire occurs (Bradstock & Cohn, 2002). Season affects seedling regeneration because of: (1) the interaction of season with the temperature requirements for seed germination and growth; (2) the interaction of the different post-fire regeneration conditions and the competition of surrounding species; and (3) the rainfall and temperature effects on seedling regeneration (Knox & Clarke, 2006). Many studies have focused on the effects of fire season on seedling emergence and survival (Hodgkinson, 1991; Sparks et al., 1998; Konstantinidis et al., 2005). The season of fire influences the amount of heat infiltrating the soil, which in turn affects soil moisture. The different seasons also influence fuel moisture and therefore fire intensity. Differences in metabolism and physiological processes between species will likewise create different responses as a result of the different burn seasons.

In this paper, we monitored the changes in the mean number of large and small seedling stems and the mean crown volume of large seedlings of hardwood regeneration one year before and after prescribed fire in oak-hickory forests. The prescribed burns were implemented three years after a shelterwood harvest was conducted in the forests, and burns were conducted in fall and spring seasons. Therefore, the objectives are to: (1) examine the effects of burn season on oak regeneration; (2) examine how the canopy of large seedlings respond to prescribed fire and thus indicate a level of competition; and (3) determine whether fire could improve the competitiveness of oak by analyzing the seedling canopy. This knowledge will help provide a better understanding of the seedling dynamics following fire.

Methods

Site and treatment descriptions

This study was conducted in Richland Furnace State Forest (RFSF; 39.171°N,

82.602°W) and Zaleski State Forest (ZSF; 39.334°N, 82.311°W) in southern Ohio. Both forests lie within the unglaciated Allegheny Plateau Region which is extensively dissected by watershed drains that exhibit undulating and rough topography. Elevation within the region ranges from the lowest

point of 180 m to the highest point of 320 m above sea level. The total annual precipitation is 104 cm, with over half of this precipitation occurring from April through September. The forests were dominated by oak and mixed hardwood species (Table 1).

Table 1. The species present in the overstory prior to harvest in the Richland Furnace State Forest and Zaleski State Forest, southern Ohio.

Upland Oak	Mixed Hardwoods	Understory	Hickory
<i>Quercus alba</i> L.	Acer saccharum Marsh.	<i>Amelanchier</i> spp.	Carya glabra (Mill.)
<i>Quercus coccinea</i> Muenchh.	<i>Acer rubrum</i> L. <i>Faqus grandifolia</i> Ehrh.	<i>Carpinus caroliniana</i> Walt.	<i>Carya laciniosa</i> (Michx. f.) Lould.
Quercus prinus L. Quercus rubra L. Quercus velutina Lam.	Fraxinus americana L. Fraxinus pennsylvanica Marsh.	Corylus americana Marsh. Hamamelis virginiana L. Lindera benzoin L.	Carya tomentosa (Poir.) Nutt.
	Liriodendron tulipifera L. Nyssa sylvatica Marsh. Populus grandidentata	Ostrya virginiana (Mill.) K. Koch Sassafras albidum (Nutt.) Nees	
	Michx. Prunus serotina Ehrh. Ulmus americana L. Ulmus rubra Muhl.	<i>Viburnum</i> spp.	

In 2005, four 10 ha treatment blocks were established in each forest to study the effects of shelterwood harvests and prescribed fire on oak and other hardwood regeneration. Two treatment blocks in each forest were established to study a fall burn three years after the shelterwood harvest and the other two blocks to study a spring burn. Plot measurements were initially taken in 2005 prior to harvests. Prior to harvest the basal area averaged 29.9 m² ha-1 with 351 trees ha-1 in RFSF, with oak and hickory accounting for 84 percent of the basal area. In ZSF, the basal area averaged 24.0 m² ha⁻¹ with 328 trees ha⁻¹, with oak and hickory accounting for 87 percent of the basal area. In 2006, the forests were thinned to approximately 50% stocking based on percent stocking determined by using stocking charts for upland hardwoods (Williams, 2003) and were still at 50% stocking at the time burns were initiated three years later (Table 2).

Table 2. Forest attributes in Richland Furnace State Forest and Zaleski State Forest in southern Ohio before and after prescribed burns. Dbh – diameter at breast height.

Time period	Forest	Basal area (m² ha ⁻¹)	Trees (ha ⁻¹)	Dbh (cm)	Stocking (%)
Before burn	Rich. Furn. SF	15.6	106	43.4	52
	Zaleski SF	15.9	129	37.1	54
After burn	Rich. Furn. SF	12.0	101	37.2	41
	Zaleski SF	9.6	120	28.1	34

Prescribed burns were implemented during the fall of 2009 and spring of 2010. Half of the treatment areas were burned on November 11, 2009 in both forests, and the remaining treatment areas in both forests were burned on March 30, 2010. Plot

measurements were taken during the late summer of 2009 prior to all burns and final measurements were taken during the late summer of 2010, allowing one growing season to occur following the burns. The burns were conducted on the same day in each forest in both the fall and spring to minimize variations of weather conditions during the burns. The burn firing methods were the same in all burns, using drip torches as the ignition source and a combined technique of ring firing and strip head firing to place the fire within the treatment areas.

Plot establishment and measurements

Each shelterwood treatment block encompassed 10 ha and was replicated four times in each forest, with two shelterwood treatments in each forest receiving fall burns and two receiving spring burns. Eight permanent circular 0.08 ha overstory plots were located within each treatment block, using a systematic scheme rather than a random approach so that plots would be evenly distributed over each treatment block. This created 32 plots in each forest for a total of 64 plots. Plots were established in 2005 prior to the shelterwood harvests, and re-measured in 2006 after harvest, again in 2007, in 2009 prior to burning and in 2010 after the burns.

On the permanent circular 0.08 ha overstory plots, all trees > 10 cm from diameter at breast height (dbh) were measured and recorded by species. A circular secondary plot 0.04 ha in size was circumscribed about the same plot center as the overstory plot for the purpose of measuring saplings $(1.3 \text{ m tall to} \le 10 \text{ cm dbh})$. A circular tertiary plot 0.02 ha in size was also circumscribed about the same plot center as the overstory plot in order to measure large seedlings (0.3 to 1.3 m height). Finally, a circular quaternary plot 0.01 ha in size was circumscribed about the same plot center as the overstory plot for the purpose of measuring small seedlings (< 0.3 m height). For this paper, data collected from the 0.02 ha large seedling plots were analyzed. On the large seedling plots, the total height, height to live crown, and major and minor axis of the seedling crown of large seedlings was measured and recorded by species to the nearest 0.05 m. However, due to time constraints, only 24 of the original 64 plots established at the outset of the study in 2005 were measured prior to the burns in 2009, accounting for 12 plots in each forest, 6 in each fall and spring burn treatment. The same plots were measured post burn in 2010 to create a series of paired plots.

Crown volume was estimated for large seedlings using the crown length and the quadratic mean of the major and minor axis of the crown. It was assumed that the average crown approximated the shape of a cone (Karlik and McKay, 2002), and the formula:

$$V = \frac{\pi d^2 L}{12} \tag{1}$$

where V = volume in m^3 , d^2 = the average crown diameter (m), and L = crown length (m), was used to estimate the crown volume of each stem. Crown length was determined by subtracting the height to the live crown of the large seedling from its measured total height. A SAS algorithm developed by Avina $et\ al.\ (2007)$ to calculate and estimate the total crown volume in different canopy strata from the ground surface up through the main canopy was used to determine the total crown volume ($m^3\ ha^{-1}$) of large seedlings.

Statistical analysis

Analysis of variance (ANOVA) was performed on the mean canopy volume per hectare and the number of stems per hectare for large seedlings between species and treatments (burn season). For analysis purposes, species were grouped into categories of interest, which included red oaks (*Quercus rubra* L., *Q. velutina* Lam., *Q. coccinea* Muenchh.), white oaks (*Q. alba* L., *Q. prinus* L.), hickories (*Carya glabra* (Mill.),

C. laciniosa (Michx. f.) Lould., *C. tomentosa* (Poir.) Nutt.), red maple and yellow-poplar. All other species were grouped into the mixed hardwoods group. Duncan's multiple range test was used to test for differences between means at the p = 0.05 level.

Results

Large seedlings

ANOVA revealed that significant differences (p = 0.05) existed among species following fall burns in the seedling canopy volume and the number of stems per hectare (Table 3). The fact that no other significant differences were detected may be the result of the relatively low sample size (n = 12 for fall burns, n = 12 for spring

burns). Duncan's multiple range test was used to determine where those differences occurred among species.

Large seedling canopy volume

Due to high variances among samples and relatively few sample plots, it was not possible to detect significant differences among samples before and after burns in most cases. We could only detect a significant increase in red maple crown volume after fall burns (Table 4). Mixed hardwoods had significantly more crown volume compared to other species before and after fall burns, and after spring burns. Mixed hardwoods experienced the greatest increase in canopy volume after fall burns, increasing by 286% (Figure 1).

On the fall burn sites, yellow-poplar ac-

Table 3. Analysis of variance statistics for large seedling (0.3–1.3 m total height) canopy volume (m³ ha-¹) and large seedling stems per hectare within each species group before and after fall and spring burns in Richland Furnace and Zaleski State Forests in southern Ohio.

Attribute	Variable	Source of variation	RMSE	F value	Pr > F
Canopy volume	Fall burn	Time relative to burn	182.01	1.99	0.1604
	Spring burn	Time relative to burn	126.23	0.01	0.9936
	Pre-burn	Burn season	106.39	0.92	0.3394
	Post-burn	Burn season	196.22	0.59	0.4453
	Fall burn	Pre-burn	60.14	2.14	0.0711
		Post-burn	234.86	2.85	0.0217
	Spring burn	Pre-burn	141.72	0.56	0.7271
		Post-burn	103.81	3.03	0.0168
Stems per hectare	Fall burn	Time relative to burn	2646.09	2.05	0.1541
	Spring burn	Time relative to burn	2488.14	0.22	0.6367
	Pre-burn	Burn season	2325.26	0.28	0.5969
	Post-burn	Burn season	2796.71	1.79	0.1837
	Fall burn	Pre-burn	2106.04	2.18	0.0669
		Post-burn	2222.38	13.25	<.0001
	Spring burn	Pre-burn	2457.37	1.06	0.3929
		Post-burn	2335.16	3.06	0.0159

Table 4. The mean¹ (standard deviation) of the total crown volume (m³ ha⁻¹) of large seedlings (0.3–1.3 m total height) for species group one year before and one year after prescribed fire by burn season (fall vs spring) in Zaleski and Richland Furnace State Forests in southern Ohio.

	Fall burn			Spring burn		
Species	Pre-burn	Post-burn	Pre-burn	Post-burn		
Red oak	24.1 (21.0)Aa	20.7 (25.3)Aa	51.4 (92.5)Aa	16.9 (17.7)Aa		
White oak	23.3 (32.7)Aa	38.3 (55.6)Aa	47.1 (108.4)Aa	43.1 (105.5)ABa		
Hickory	15.9 (19.3)Aa	6.6 (9.0)Aa	11.2 (9.1)Aa	14.3 (14.2)Aa		
Red maple	40.2 (49.8)ABa	96.4 (70.2)Ab	50.9 (51.0)Aa	128.0 (140)Ba		
Yellow-poplar	62.9 (119.4)ABa	32.3 (64.9)Aa	97.7 (306.1)Aa	20.6 (80.9)Aa		
Mixed Hardwoods	79.9 (57.3)Ba	308.9 (194.2)Ba	92.3 (104.8)Aa	126.6 (114.0)Ba		

¹Means followed by the same capital letter are not significantly between species within burn season (fall/spring) and time relative to burn (pre-burn/post-burn). Means followed by the same small case letter are not significantly different between time relative to burn within species and burn season, Duncans MRT (p = 0.05).

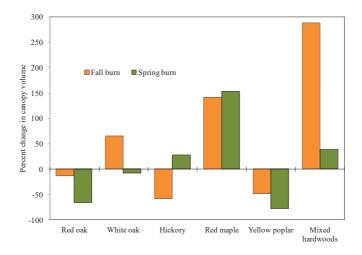


Figure 1. The percent change in large seedling (0.3–1.3 m total height) canopy volume (m³ ha⁻¹) after fall and spring burns in Richland Furnace and Zaleski State Forests of southern Ohio.

counted for 26% of the total canopy volume, and together with red maple and mixed hardwoods, accounted for 74% of the total canopy volume prior to burns on the fall burn sites (Table 4). However, after the fall burns, yellow-poplar accounted for only 6% of the total seedling canopy while red maple and mixed hardwoods combined accounted for 81% of the total canopy volume.

On the spring burn sites, yellow-poplar accounted for 28% of the total canopy volume, and combined with red maple and mixed hardwoods accounted for 69% of the total canopy volume. After the spring burns, yellow-poplar was reduced to 6% of the total volume while red maple and mixed hardwoods made up 74% of the total volume.

Both fall and spring burns reduced the red oak canopy volume, with spring burns reducing the volume by a greater magnitude (Figure 1). Fall burns reduced the red oak canopy by 14% while spring burns reduced the canopy by 67% (Table 4). Prior to fall burns, red oak comprised 10% of the total canopy and was reduced to 4% of the total canopy after the burns. Prior to spring burns the red oak canopy made up 15% of the total canopy but was reduced to 5% of the total canopy following the burns.

White oak accounted for 9% and 13% of the total canopy prior to burning on the fall burn and spring burn sites, respectively (Table 4). Spring burns reduced the white oak canopy by only 8%, accounting for 12% of the total canopy following the burns. However, fall burns increased the volume of white canopy by 64%; but because of the increased mixed hardwood and red maple canopy, the white oak seedling canopy occupied a lower percentage of the total seedling canopy than before the burn (Figure 1).

Fall burns resulted in a decrease in hickory canopy volume by 59% (Figure 1). This reduced hickory from 6% of the total seedling canopy to 1% (Table 4). Spring burns on the other hand increased the hickory canopy volume by 27%. This increase resulted in changing hickory from comprising 3% of the total seedling canopy prior to the burns, to 4% of the total seedling canopy after the burns.

Large seedling stems per hectare

Prior to the burns, significantly more yellow-poplar and mixed hardwood stems occurred on sites where fall burns were to be executed, accounting for 52% of total stems (Table 5). Yellow-poplar and mixed hardwoods accounted for 25% and 27% of total stems, respectively. After fall burns, mixed hardwood stems increased significantly by 141%, and were significantly higher than all other species (Figure 2). Mixed hardwoods accounted for 48% of total stems after the fall burns. Yellow-poplar on the other hand was reduced by 64% after the fall burns, comprising 7% of total stems after the fall burns. Similarly, yellow-poplar was reduced by 61% after spring burns, thereby decreasing its percent composition of total stems from 19% prior to spring burns to 7% of total stems following burns.

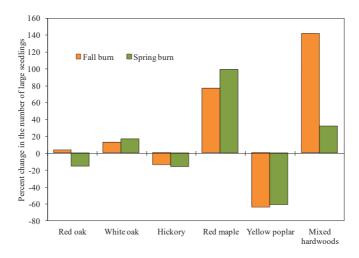


Figure 2. The percent change in the number of large seedling (0.3–1.3 m total height) stems per hectare after fall and spring burns in Richland Furnace and Zaleski State Forests of southern Ohio.

Table 5. The mean¹ (standard deviation) of the number (stems per hectare) of large seedlings (0.3–1.3 m total height) for species group one year before and one year after prescribed fire by burn season (fall vs spring) in Zaleski and Richland Furnace State Forests in southern Ohio.

	Fall burn		Spring burn		
Species	Pre-burn	Post-burn	Pre-burn	Post-burn	
Red oak	1334 (1039)ABa	1379 (725)ABa	1334 (1137)Aa	1127 (894)ABa	
White oak	1503 (1451)ABa	1688 (1721)ABa	1733 (2629)Aa	2021 (3185)ABCa	
Hickory	325 (267)Aa	280 (354)Aa	373 (252)Aa	314 (219)Aa	
Red maple	1758 (1596)ABa	3100 (2072)Ba	1302 (1251)Aa	2582 (1891)ABCa	
Yellow-poplar	2589 (3978)Ba	926 (1216)ABa	1725 (4476)Aa	674 (1878)ABa	
Mixed hardwoods	2783 (1903)Ba	6710 (3566)Cb	2686 (2530)Aa	3543 (3828)Ca	

¹Means followed by the same capital letter are not significantly different between species within burn season (fall/spring) and time relative to burn (pre-burn/post-burn). Means followed by the same small case letter are not significantly different between time relative to burn within species and burn season, Duncans MRT (p = 0.05).

Red maple displayed a 76% increase after the fall burns, accounting for 22% of total stems after the burns, compared to 17% before the burns. Spring burns produced a more favorable response of red maple, increasing its numbers by 98% (Figure 2). Prior to spring burns red maple accounted for 14% of the total stem composition, which subsequently increased to 25% of the total composition following the spring burns (Table 5).

Very little change occurred in the number of red oak stems following fall burns, and spring burns reduced the number of stems by 16% (Figure 2). In spite of the small increase in the number of red oak stems after fall burns, red oak was reduced compared to the total of regenerating stems, dropping from 13% of total stems before the burns to 10% after the burns (Table 5).

White oak experienced an increase in the number of stems after both fall and spring burns, increasing by 12% and 16%, respectively (Figure 2). The increase that occurred after spring burns was enough to raise the number of white oak stems representing the total stems from 19% to 20%. However, the increase in white oak stems after fall burns was not enough to increase

its component of total stems, as it dropped from 14% of total stems prior to burning to 12% after burning.

Hickory remained a very small fraction of the total seedling composition before and after fall and spring burns (Table 5). Prior to the burns, hickory accounted for 3% and 4% of total stems on the fall and spring burn sites, respectively. Following the burns, these figures dropped to 2% and 3% of total stems after fall and spring burns, respectively. Hickory experienced a 3% increase in stems after fall burns, but displayed a 16% decrease after spring burns (Figure 2).

Importance value index

The importance value index (IVI) (Curtis, 1959) of large seedlings for each species group was calculated (Table 5). IVI for a species is typically determined by the average of relative frequency, relative density and relative basal area as an indicator of the amount of area each species occupies relative to other species. However, in this paper, the relative crown volume was used instead of relative basal area as an indicator of occupied space.

Prior to fall and spring burns, yellow-poplar and mixed hardwoods were

the top two dominant species groups based on IVI (Table 6). Following both fall and spring burns, mixed hardwoods remained as first importance in the seedling population, but yellow-poplar fell to next to last (ahead of hickory) after fall burns, and last after spring burns. Red maple took yellow-poplar's place in dominance following fall and spring burns, behind the mixed hardwoods.

Table 6. The Importance Value Index¹ for large seedlings (0.3–1.3 m total height) by species groups and burn season one year before and after prescribed fire in Zaleski and Richland Furnace State Forests of southern Ohio. The Importance Value Index ranking is indicated in the parenthesis.

	Fall burn		Spring burn		
Species group	Pre-burn	Post-burn	Pre-burn	Post-burn	
Red oak	115.1 (5)	113.9 (4)	111.1 (4)	115.8 (4)	
White oak	116.4 (4)	119.6 (3)	114.2 (3)	122.9 (3)	
Hickory	101.9 (6)	87.9 (6)	89.1 (6)	107.2 (5)	
Red maple	125.7 (3)	141.2 (2)	110.6 (5)	161.8 (2)	
Yellow-poplar	143.0 (2)	97.61 (5)	119.4 (2)	76.1 (6)	
Mixed hardwoods	151.8 (1)	209.0 (1)	146.6 (1)	170.8 (1)	

¹Seedling crown volume was used in the calculation instead of basal area to determine relative dominance.

Fall and spring burns did little to change the dominance of oak and hickory species (Figure 3). Spring burns did create an increase in the dominance of oak and hickory in the regeneration layer, but also a much greater increase in the dominance of red maple. Red maple displayed the largest increase in importance after spring burns compared to other species. In fact, spring burns caused an increase in the relative dominance of all species groups, except for yellow-poplar.

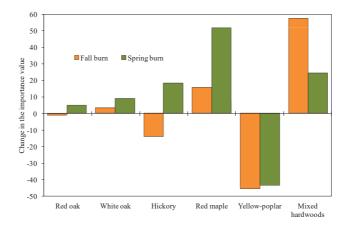


Figure 3. The change in magnitude of the Importance Value Index for selected species groups of large seedlings (0.3–1.3 m total height) after fall and spring burns in Richland Furnace and Zaleski State Forests located in southern Ohio. Seedling crown volume was used in the calculation instead of basal area to determine relative dominance.

Fall burns had a more mixed effect, reducing the dominance of red oak, hickory and yellow-poplar and increasing the dominance of white oak, red maple and mixed hardwoods (Figure 3). Fall burns caused the greatest increase in dominance for mixed hardwoods, and the greatest decrease in the dominance of yellow-poplar.

Discussion

The time of year a burn is executed can result in different responses by a species. When the fall burns were executed (November), rootstocks contained higher carbohydrate reserves compared to diminished reserves during spring burns (Hodgkins, 1958; Ferguson, 1961; Brose & Van Lear, 1998). In addition, cell activity, including the cambium, diminishes or becomes dormant by late fall. This combination allows seedlings to better withstand fall fires and respond more positively to growth in the spring (Drewa et al., 2002). Conversely, in the spring the carbohydrate reserves have begun to migrate out of the rootstocks and cells become more active, making seedlings more vulnerable (Hodgkins, 1958; Langdon, 1981; Garrison, 1972; Hough, 1968; Volland & Dell, 1981; Bond & van Wilgen, 1996; DeBano et al., 1998). Rootstocks are also more likely to survive fire when seedlings are dormant (Cain & Shelton, 2000).

Oak species as a whole tend to be less susceptible to fire during the dormant season, such as late fall or early winter burns (Rouse, 1986; Rundel, 1980). In our study we found that spring burns appeared to be more detrimental to red oak than fall burns, although we found no significant difference. Red oak displayed greater reductions in canopy volume and stem numbers after spring burns compared to fall burns. Van Lear & Waldrop (1988) reported that a spring fire killed 58% of existing red oak seedlings, and failed to increase oak abundance in the understory. North-

ern red oak seedlings are easily killed by prescribed fires and only the larger stems will sprout and survive, even if their tops are killed (Johnson, 1974). Spring burns occur about the time of red oak germination, and thus recruitment of new individuals could be somewhat challenging.

Fall burns, on the other hand, seemed to have only a slightly more positive effect on white oak. Compared to spring burns, there was an increase in the seedling canopy volume while spring burns resulted in a slight reduction. Both fall and spring burns created a small increase in the number of regenerating white oak stems. The white oak species tended to outperform the red oak species with respect to establishment of post-fire regenerating stems, seedling canopy and IVI, although the differences were marginal. This seems to be consistent with Fan et al. (2012) in their study of repeated burns in upland oak-hickory forests in Missouri. While white oak gained in its dominance based on IVI in the large seedling layer after fall and spring fires, red oak lost some dominance after spring burns. However, the change in IVI was never large enough for either white or red oak to change in their dominance relative to other species.

However, based on IVI, spring burns had more of a positive impact on large seedlings than fall burns. All species, with the exception of yellow-poplar, experienced an increase in importance, or relative dominance. This may be in part a result of mixed hardwoods not experiencing as large of an increase in dominance as it did after fall burns, and the large decrease in IVI that yellow-poplar experienced. The canopy volume and stem number increase of mixed hardwoods after spring burns was much lower than after fall burns, and the reduction in the seedling canopy volume of yellow-poplar was greater after spring burns.

While mixed hardwoods were represented by many different species, sassafras (Sassafras albidum (Nutt.) Nees) and black-

gum (Nyssa sylvatica Marsh.) tended to dominate this component of the regeneration layer. While both fall and spring burns increased the number and canopy volume of large mixed hardwood seedlings, fall burns produced higher amounts compared to spring burns. Both sassafras and blackgum respond positively to fire (Iverson et al., 2008). Sassafras sprouts prolifically after top-killed by fire (Cole et al., 1990) and also displays lower mortality rates after fire compared to that of other hardwoods (Apfelbaum & Haney, 1990). Season of burn does not appear to have as much of a discriminatory effect on sassafras as it does on many other hardwoods (de Bruyn & Buckner, 1981). Blackgum likewise sprouts prolifically after top-killed by fire (Keetch, 1944), and eventually succumbs to fire only after repeated burns (Waldrop et al., 1987).

Both fall and spring burns resulted in an increase in the seedling canopy volume and stems per hectare for red maple. Red maple experienced the greatest increase in canopy volume and stems per hectare after spring burns. While we did not record whether a stem was of sprout origin or not, it is probable that the majority of stems in the large seedling size category was of sprout origin, either from top-killed seedlings or as sprouts from stumps produced during the shelterwood harvest. Red maple can sprout vigorously after fire when seedlings are top-killed, including those growing as sprouts from cut stumps (Scheiner et al., 1988; Swan, 1970; Walters & Yawney, 1990). Even though it is likely our sample size did not allow us to detect significant changes, the number of red maple stems increased by 76% and by 98% after fall and spring burns, respectively. The regrowth of red maple after fire can be rapid, and combined with its prolific sprouting ability, can create a high stem density that promulgates its dominance in a stand (Martin, 1955; Tirmenstein, 1991; Hutnick & Yawney, 1961). While it is possible for prescribed fire to reduce the number of regenerating red maple stems, particularly fires of moderate intensity, those that do survive tend to show greater height growth after fire than oak seedlings (Green et al., 2010), thereby producing a larger number of large seedlings and increasing the seedling canopy. Even though Brose & Van Lear (1998) found that spring and summer fires reduced the densities of red maple more than winter burns, we found no significant differences between burn seasons, and we discovered that red maple density increased in both cases. The reports of the effects of fire on red maple have been variable, with some reporting reduced densities (Reich et al., 1990; Elliott et al., 1999), while others report increased densities (Blankenship & Arthur, 2006).

In comparison to the oak species, both fall and spring burns increased the competitiveness of red maple and the mixed hardwoods. If we look at the seedling canopy, we find that the ratio of the oak seedling canopy to the red maple seedling canopy dropped from 1.18 before fall burns to 0.61 after fall burns. After spring burns, the ratio has a greater reduction, dropping from 1.93 before burns to 0.47 after burns. In both cases the combined oak seedling canopy volume was greater than that of red maple seedling canopy before the burns, thereby suggesting that oak species were in a competitive position in comparison to red maple prior to burning.

On the spring burn sites, the oak canopy volume was almost equal to that of the mixed hardwoods, and a little more than half of the mixed hardwoods on the fall burn sites. The ratio of the oak seedling canopy to the mixed hardwood canopy prior to spring and fall burns was 1.07 and 0.59, respectively. These ratios dropped to 0.47 and 0.19 after spring and fall burns, respectively.

While both red maple and oak will resprout after fire, their responses are physiologically different. Oak seedlings put more carbon and energy into storage and roots while red maple directs more of this energy into height growth (Brose & Van

Lear, 1998, 2004; Huddle & Pallardy, 1999; Reich et al., 1990). This difference in energy allocation enables oak to survive repeated fires, but enables red maple to maintain height growth advantage over oak after repeated fires (Green et al., 2010). Hence, we found that the red maple seedling canopy was dominant over oak after both fall and spring burns, second only to the mixed hardwood group. When a disturbance occurs that increases the understory light, such as after shelterwood harvests and prescribed fire, red maple will produce new leaves rapidly as a response since they are thin with few secondary compounds (Nagel et al., 2002). However, repeated burns have demonstrated to reduce red maple density (Blankenship & Arthur, 2006) while at the same time, frequent repeated burns have shown not to increase oak regeneration consistently (Hutchinson et al., 2005).

Both fall and spring burns reduced the number of large yellow-poplar seedlings and the seedling canopy. Yellow-poplar seedlings and saplings have thin bark which makes them very susceptible to fire damage, and fire generally kills young trees less than 2.5 cm in diameter (Beck, 1990). However, yellow-poplar seedlings can sprout from the root crown if topkilled by fire (Kelty, 1988). Nevertheless, mortality rates of large seedlings were higher than regenerative rates, and fall burns caused these mortality rates to be slightly higher. Accordingly, the ratio of the oak seedling canopy volume to that of yellow-poplar increased after both fall and spring burns. After fall burns the ratio increased from 0.75 to 1.83 and after spring burns increased from 1.01 to 2.91. Both burns decreased any competitive advantage that yellow-poplar had over oak, reducing not only the canopy volume but also the number of regenerating stems. It has been reported that regardless of fire season, yellow-poplar densities are decreased as a result of fire.

Hickory was present in the regeneration layer prior to fall and spring in relatively few numbers, and its dominant position based on IVI was last prior to both fall and spring burns. After fall burns, the hickory IVI value dropped from 101.91 to 87.91, keeping it the least dominant of the six species groups studied. Fall burns not only decreased the number of regenerating stems but also the volume of the seedling canopy. Spring burns likewise reduced the number of regenerating hickory stems, but increased the seedling canopy volume. Accordingly, after spring burns the hickory IVI increased from 89.10 to 107.16, making it next to last after yellow-poplar.

Even though oak did not display a significant positive response to fire, it may be the response of its competitors that eventually cause the restoration of these oak systems to occur. The change in the composition and structure of eastern deciduous forests, and oak-dominated forests in particular, have been linked to long periods of fire suppression as well as the loss of the American chestnut (Castanea dentata (Marsh.) Borkh.) and changes in harvesting methods (Blankenship & Arthur, 2006). Consequently, it is unlikely that a single burn after a shelterwood harvest will bring the forest back to its natural composition and structure. Reintroducing fire into these systems at a higher than normal periodicity may be what is necessary to restore these systems. Studies have demonstrated mixed results of fire on oak regeneration (Fan et al., 2012) and continued research is necessary to further understand the role of fire and other disturbances in these ecosystems, and how they can be used in management and restoration efforts.

Conclusions

Three years after a shelterwood harvest the effects of fall and spring burns on large hardwood seedlings were evaluated by examining the seedling canopy volume and the number of stems per hectare. Based on these evaluations, our study reveals that if regenerating oak and putting it into a competitive position in the regeneration layer is a management objective, then it will require more stand treatments than a single fire following a shelterwood harvest. Red maple and mixed hardwoods dominated the large seedling layer after both fall and spring burns based on the number of regenerating large seedlings and their total crown volumes. We did not detect any significant advantage that a single fall or spring burn created for oak.

Fall and spring burns appeared to be more deleterious to red oak than white oak. Red oak experienced reductions in numbers and canopy volume after spring burns, and canopy reductions after fall burns. There was only a marginal increase in red oak numbers after fall burns. White oak experienced small increases in the numbers of stems after both fall and spring burns, and an increase in the canopy volume after fall burns, but a slight decrease after spring burns. Yellow-poplar, a major oak competitor prior to fire, experienced dramatic reductions in the number of regenerating stems and canopy volume.

The fact that there were no dramatic changes in oak after fire compared to other species could become an advantage for oak in the future. The oak population remained relatively stable after both fall and spring burns, while other species, including red maple and yellow-poplar, experienced dramatic shifts. Yellow-poplar displayed high mortality after one burn, and it is likely that repeated burns will continue to keep this species at bay. Red maple on the other hand appeared to benefit from these burns.

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