NRC Research Press

ARTICLE

Reversing legacy effects in the understory of an oak-dominated forest

Melissa Thomas-Van Gundy, James Rentch, Mary Beth Adams, and Walter Carson

Abstract: Current forests developed under conditions different from original forests, with higher deer densities, reduced fire frequency, denser canopies, and smaller canopy gaps. These alterations have led to understories dominated by species simultaneously browse tolerant, shade tolerant, and fire sensitive leading to difficulties in the regeneration of oak species (*Quercus* spp.) in some areas. We evaluated how three key processes — understory fire, canopy gaps, and browsing — influenced tree species in east central West Virginia. We were particularly interested in the response of oak species because they are the dominant overstory species and of maple species (*Acer* spp.), black birch (*Betula lenta* L.), and yellow-poplar (*Liriodendron tulipifera* L.) as these are likely to replace the current forest. Single-process effects were significant and significant interactions among processes were numerous. In general, fire caused significant reductions of seedlings and saplings of red maple (*Acer rubrum* L.) and striped maple (*Acer pensylvanicum* L.) and increased the seedlings of black birch and yellow-poplar. Canopy gaps increased the abundance of black birch and yellow-poplar seedlings and saplings. Gaps and fire together caused an increase in the relative abundance of yellow-poplar. Excluding browsers and creating canopy gaps together nearly doubled oak sapling importance values versus either treatment alone; however, oak importance values remained low. Given the significant interactions of browse control with the other two processes, browse control should be considered when planning oak regeneration treatments such as canopy gaps or prescribed fire.

Key words: disturbance ecology, succession, deer browse, prescribed fire, regeneration.

Résumé : Les forêts actuelles se sont développées sous des conditions différentes de celles des forêts d'origine, soit une densité plus élevée de cerfs, une fréquence de feu plus faible et un couvert forestier plus dense comportant de plus petites trouées. Ces modifications ont produit des sous-étages dominés par des espèces simultanément tolérantes au broutement, tolérantes à l'ombre et sensibles au feu, ce qui a causé des problèmes de régénération des espèces de chêne à certains endroits. Nous avons déterminé de quelle façon trois processus clés : les feux en sous-étage, les trouées dans le couvert forestier et le broutement, ont influencé la présence d'espèces d'arbre dans le centre-est de la Virginie occidentale. Nous étions particulièrement intéressés par la réaction des espèces de chêne, parce qu'elles sont les espèces dominantes du couvert, et par les érables, le bouleau noir et le tulipier de Virginie, parce que ces espèces remplaceront probablement les espèces dominantes actuelles. Les effets simples des processus étaient significatifs et les interactions significatives entre les processus étaient nombreuses. En général, le feu a significativement réduit le nombre de semis et de gaules d'érables rouge et de Pennsylvanie, et a augmenté le nombre de semis de bouleau noir et de tulipier de Virginie. Les trouées dans le couvert forestier ont causé une augmentation de l'abondance des semis et des gaules de bouleau noir et de tulipier de Virginie. L'effet combiné des trouées et du feu a causé une augmentation de l'abondance relative du tulipier de Virginie. L'exclusion du broutement conjuguée à la création de trouées dans le couvert forestier a presque fait doubler la valeur d'importance (VI) des gaules de chêne par rapport à l'effet de ces deux traitements pris séparément. Toutefois, la VI du chêne est demeurée faible. Étant donné les interactions significatives entre la maîtrise du broutement et les deux autres processus, la maîtrise du broutement devrait être considérée lors de la planification des traitements de régénération des chênes tels que les trouées dans le couvert forestier et le brûlage dirigé. [Traduit par la Rédaction]

Mots-clés : écologie des perturbations, succession, broutement par le cerf, brûlage dirigé, régénération.

Introduction

Oak (*Quercus* spp.) -dominated forests in the central hardwood region of the eastern United States, once thought to be self-perpetuating, have shown declines in overstory oak abundance both in managed and unmanaged forests (Abrams and Downs 1990; Nowacki et al. 1990; Galbraith and Martin 2005; Fei et al. 2011). These declines include regional failures of oak species to regenerate on all but the most xeric sites (Lorimer 1989; Abrams 1992). On more mesic sites oaks are often replaced either by shade-tolerant species, such as maple (*Acer* spp.) or American beech (*Fagus grandifolia* Ehrh.), present in the understory at the time of disturbance or by species such as black birch (*Betula lenta* L.) and yellow-poplar (*Liriodendron tulipifera* L.) that respond to disturbances such as timber harvest (Lorimer 1984; McGee 1986; McCarthy et al. 1987; Crow 1988; Loftis 1990; Nowacki et al. 1990; Brashears et al. 2004; Nowacki and Abrams 2008).

Oak forests have dominated the central hardwood region for thousands of years (Watts 1979; Davis 1981) even following disturbances including clearing for agriculture, extensive and exploitative logging and slash fires (Stephenson 1993), and the loss of key species from disease (Woods and Shanks 1959). In general, current

Received 13 September 2013. Accepted 18 December 2013.

M. Thomas-Van Gundy and M.B. Adams. Northern Research Station, USDA Forest Service, PO Box 404, Parsons, WV 26287, USA.
J. Rentch. Division of Forestry and Natural Resources, West Virginia University, PO Box 6125, Morgantown, WV 26506-6125, USA.
W. Carson. Department of Biological Science, 4249 Fifth Avenue, Pittsburgh, PA 15260, USA.

Corresponding author: Melissa Thomas-Van Gundy (e-mail: mthomasvangundy@fs.fed.us).

Can. J. For. Res. **44**: 350–364 (2014) dx.doi.org/10.1139/cjfr-2013-0375

forests exist under altered conditions from those that original forests developed under, with higher deer densities (Rooney 2001), reduced fire frequency (Nowacki and Abrams 2008), denser canopies, less flammable understories (Nowacki and Abrams 2008), and smaller canopy gaps (Clebsch and Busing 1989). These alterations have led to depauperate understories dominated by a few tree species that are simultaneously browse tolerant, shade tolerant, and fire sensitive (Kain et al 2011; Nuttle et al. 2013) and species composition trajectories that are counter to classical succession theory (e.g., McGee 1986; Nowacki and Abrams 1992, 2008; Galbraith and Martin 2005; Fei and Steiner 2007; Nuttle et al. 2013).

Replacement of canopy oaks is largely dependent on seedlings and saplings present as advance regeneration (Sander and Clark 1971; Sander 1972; for review of oak ecology see Johnson et al. 2009). While oaks may still be found in the understory as small seedlings, oaks no longer appear to have the ability to persist in the understory for decades as they did during the past 350 years (McGee 1986; Abrams and Downs 1990; Nowacki and Abrams 1992; Rentch et al. 2003; Hart and Grissino-Mayer 2009). Experimental thinning of the midstory together with the planting of oak seedlings in a forest in Wisconsin demonstrated that a tall, shade-tolerant understory prevents oak seedlings from entering larger sapling size classes that might then be capable of reaching the canopy (Lorimer et al. 1994). This bottleneck between seedling and sapling stages is a common pattern in oak-dominated forests in transition to fire-sensitive and shade-tolerant species composition (Lorimer et al. 1994).

Lorimer (1989) argued that a reduction in fire frequency could explain increases in the abundance of shade-tolerant tree species under oak-dominated canopies. With adaptations to disturbance and water stress, oaks possess traits that enhance survival following repeated fire. In general, mature oaks have thick bark (Harmon 1984), resprout from root collar buds after top kill (Waldrop and Lloyd 1991; Huddle and Pallardy 1999; Peterson and Reich 2001), have a deep root system (Hinckley et al. 1981), and the ability to compartmentalize stem injury and resist rotting (for reviews see Lorimer 1989; Abrams 1990, 1992). Prescribed fires can promote oak regeneration by reducing interfering vegetation (Arthur et al. 1998; Barnes and Van Lear 1998; Signell et al. 2005; Blankenship and Arthur 2006; Iverson et al. 2008) or increasing root/shoot ratios of oaks after top kill (Johnson 1993; Barnes and Van Lear 1998).

In contrast, other studies have found little positive impact of fire on oak species. For example, Collins and Carson (2003) reported that not only did oaks rarely resprout after fire they also resprouted less often than co-occurring species (e.g., red maple (*Acer rubrum* L.)). In addition, red maple individuals that survived prescribed fire showed greater height and diameter growth than surviving oak seedlings (Alexander et al. 2008; Green et al. 2010). Repeated burning did not result in changes in oak and hickory (*Carya* spp.) seedling density even though repeated fire did reduce total sapling density (Hutchinson et al. 2005). Single burns have failed to control striped maple (*Acer pensylvanicum* L.) and caused unacceptable damage to overstory trees (Wendel and Smith 1986) while resulting in no change in small oak seedling densities (Albrecht and McCarthy 2006). In contrast, in a recensus of a study involving a single prescribed fire after shelterwood harvest, Brose (2010) found that increases in oak stems per hectare and decreases in red maple and yellow-poplar seen 2 years post fire (Brose and Van Lear 1998) persisted into the 11th year post fire. Also, 11 years after one prescribed fire, the number of dominant oak and hickory saplings (defined as the tallest stem on a plot) increased with increasing fire intensity as the numbers of dominant red maple and yellow-poplar decreased (Brose 2010). This work (Brose 2010) also demonstrates the effect of canopy removal combined with prescribed fire on oak regeneration. In a study of burned and unburned canopy gaps formed by a natural mortality event, only the combination of canopy gaps and repeated prescribed fires caused significant increases (6 times) in the numbers of large oak and hickory stems compared with unburned gaps (Hutchinson et al. 2012). In this study, where canopy gaps were not experimentally created, prescribed fire occurred before and after gap formation leading to questions of not only the contributions of fire and canopy gaps to successful oak regeneration but also the timing of each disturbance.

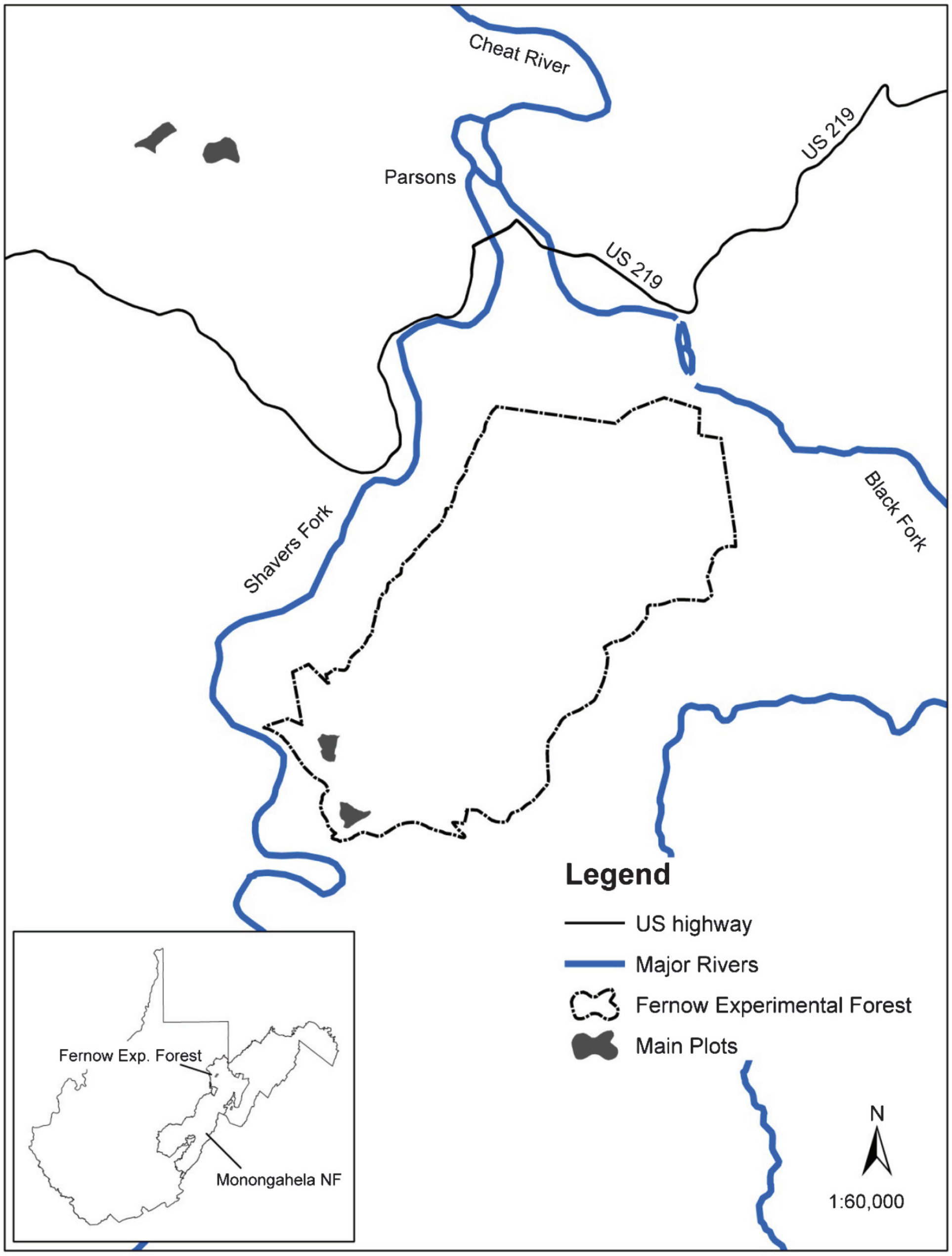
Timber harvests and natural disturbances create canopy gaps of various sizes that increase understory light levels. Large canopy gaps may increase overall tree species diversity by creating conditions allowing for shade-tolerant and intermediate-tolerant species to coexist (Runkle 1981; Clebsch and Busing 1989; Rentch et al 2003). In contrast, smaller canopy gaps are often captured by the lateral expansion of established trees (Clebsch and Busing 1989) or by shade-tolerant advance regeneration and sprouts (Canham et al. 1994; Dietze and Clark 2008). Natural canopy gaps in second-growth forests tend to be smaller than gaps in old-growth forests because of the smaller crowns of canopy trees (Clebsch and Busing 1989). In unburned oak-dominated forests, these smaller gaps are typically filled in by the lateral extension of the surrounding canopy or by shade-tolerant species present as advance regeneration (Cowell et al. 2010; Hutchinson et al. 2012). Oaks are intermediate in shade tolerance and as such generally require larger canopy gaps to attain overstory status. Silvicultural guidelines for the oak–hickory forest type suggest openings of at least 0.2 ha; however, openings as small as 0.04 to 0.1 ha should perpetuate existing oak advance regeneration or stump sprouts (Sander et al. 1983). Thus, gaps, both natural or as a result of harvests, in second-growth oak-dominated forests may not promote the coexistence of pioneer species or species intermediate in shade tolerance, particularly oaks.

Deer are a keystone species because they reduce the abundance of some tree species relative to others, often reducing diversity and changing the species composition of the advance regeneration layer (Rooney 2001). Female deer have high site fidelity, low dispersal rates (Campbell et al. 2004), and overlapping home ranges of offspring (Porter et al. 1991; Campbell et al. 2004), and browsing can cause changes in tree species composition even at relatively low numbers ($>\sim 8$ deer/km^2) (Horsley et al. 2003). In addition, deer are selective foragers and tree species vary widely in browse tolerance and palatability (Horsley et al. 2003; Côté et al. 2004); consequently, browsing can create understories that are dominated by unpalatable or browse-tolerant species that can change the expected impacts of fire or large canopy gaps (Nuttle et al. 2013). Thus, browse tolerance may be as, or more, important than shade tolerance in determining the composition of the advance regeneration layer (Long et al. 2007; Krueger et al. 2009; Nuttle et al. 2013).

Here we evaluate how three key processes — surface fire, canopy gaps, and browsing — alter forest regeneration using a full factorial experimental design on the Fernow Experimental Forest (FEF) and the Monongahela National Forest (MNF) in West Virginia. We examined the responses of the common species of seedlings and saplings including sugar (*Acer saccharum* Marsh.), red, and striped maple, yellow-poplar, black birch, and oaks (northern red (*Quercus rubra* L.), chestnut (*Quercus prinus* L.), white (*Quercus alba* L.), and black oak (*Quercus velutina* Lam.)) to surface fire, browsing, and gaps. We were particularly interested in the response of oak species because they are the dominant overstory species. The responses of the maple species, black birch, and yellow-poplar are important as these are likely to replace the current oak forest after stand-level disturbances such as timber harvest (McGee 1986; Abrams and Downs 1990; Fei and Steiner 2007; Fei et al. 2011; Schuler et al. 2013).

Our study design allows for the testing of interactions among these three key processes. Others have shown that fire and canopy gaps together increased herb layer richness and abundance more

Fig. 1. General study area and locations of main plots.



than fire and canopy gaps alone (Royo et al. 2010). However, in the absence of browse pressure, palatable species dominated areas with canopy gaps and fire leading to lower species richness (Royo et al. 2010). We expect interactions also will apply to the seedling and sapling layers; however, the role of browse may be different for tree species and as saplings grow out of browse range. In an area where deer were considered overabundant, one prescribed fire resulted in significant reductions in density, richness, and diversity of saplings in unfenced areas (Nuttle et al. 2013). Returning fire and large canopy gaps to forests without controlling herbivory may not increase seedling and sapling species diversity and is likely to create depauperate understories after fire (Nuttle et al. 2013).

Methods

Study area and experimental design

The study sites were located on the FEF and the MNF near Parsons, West Virginia, in the western Allegheny Mountains ecological subsection (Cleland et al. 2007) and were dominated by a mixed mesophytic hardwood forest (Fig. 1). The area receives an annual mean of 1430 mm of precipitation distributed evenly throughout the year (Pan et al. 1997). The two FEF study plots range in elevation from 670 to 790 m with one site facing southeast and the other west. The two study plots on the MNF range in elevation from approximately 670 to 760 m and have generally north to west aspects. The study plots are in upland locations and include side slopes and ridge landforms. Study areas were 10 to 40 ha in size. These four areas are termed main plots with treatments applied at this level and the subplot level.

The study areas were minimally managed second-growth stands (between 60 and 90 years old) with overstories dominated by northern red and white oak and sugar and red maple (Table 1). Other canopy species included at the time treatments were applied were yellow-poplar, American beech, black cherry (*Prunus serotina* Ehrh.), and black birch. Before treatment, maples, mainly striped

Table 1. Study area composition pre-treatment (1999) summarized by plot locations.

	Stems/ha			Basal area/ha (m^3/ha)			Stems/ha
Species	Saplings	Overstory	Total	Saplings	Overstory	Total	Seedlings (>20 cm)
FEF							
Maple	361	207	568	1	9	10	7 817
Black birch	2	5	7	0	0.5	0.5	130
American beech	52	8	60	0	0	0	290
White ash	2	8	10	0	1	1	140
Yellow-poplar	1	22	22	0	2	2	0
Magnolia	6	6	12	0	0	0	227
Black cherry	0	6	6	0	1	1	83
Oaks	1	95	96	0	22	22	3 420
Hickory	2	14	15	0	1	1	0
American chestnut	1		1	0		0	10
Grapevine	23		23	0		0	197
Mtn. laurel and rhododendron	6		6	0		0	17
Blueberry							40
Other shrubs	4		4	0		0	47
Other trees	12	19	31	0	1	1	1 780
Other vines							10
Total	473	388	861	2	38	40	14 207
MNF							
Maple	685	130	815	2	6	8	19 721
Black birch	6	5	11	0	0	0	7
American beech	19	4	22	0	0	0	146
White ash	7	1	8	0	0	0	582
Yellow-poplar	9	11	20	0	1	1	4
Magnolia	11	6	17	0	0	0	54
Black cherry	24	0	24	0	0	0	118
Oaks	13	173	186	0	24	25	10 893
Hickory	24	21	45	0	1	1	571
American chestnut	17		17	0		0	1 464
Grapevine	1		1	0		0	32
Mtn. laurel and rhododendron	1		1	0		0	821
Blueberry			0			0	1 339
Other shrubs	36		36	0		0	818
Other trees	184	12	196	0.5	0	1	6 221
Other vines			0			0	18
Total	1 038	362	1 400	3	33	36	42 811

Note: Two study plots are on the Fernow Experimental Forest (FEF) and two on the Monongahela National Forest (MNF). Saplings are defined as stems with a diameter at breast height (dbh) of 2.5–12.7 cm; overstory stems are those greater than 12.7 cm in dbh.

maple, dominated the sapling and seedling components of these stands (Table 1). No logging occurred in the study sites within 27 years prior to the start of this study in 1998; one plot on the MNF was thinned in 1972. Deer density in the area of the study (county-level data) is estimated at 11–17 deer/km^2 (QDMA 2010) but was estimated to be 6 deer/km^2 for the FEF (Adams et al. 2004).

Fire, gap, and browse effects were controlled for in a split-plot factorial design (see Royo et al. 2010; Nuttle et al. 2013). Within each of the four main plots, there are sixteen 20 m by 20 m (400 m^2) subplots located at least 20 m from each other and 20 m from stand edges, fire breaks, recent canopy gaps, and large rock outcrops. One half of each main plot was randomly designated to be burned. Within each half, two subplots were randomly assigned to a fence, gap, fence plus gap, or control treatment resulting in a total of 64 subplots with treatments of Fire, Fence, Gap, Fence + Gap, Fire + Fence, Fire + Gap, Fire + Fence + Gap, or Control (Fig. 2).

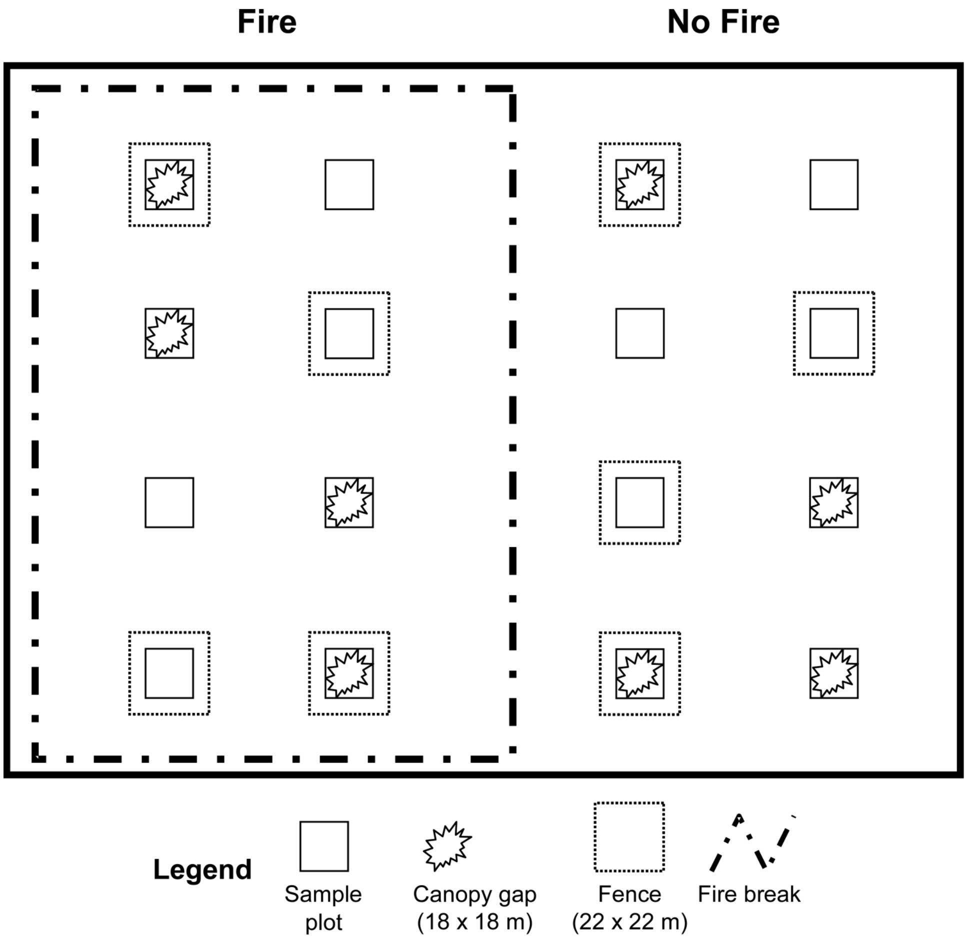
Plots were established in 1998 and initial data collected in 1999 prior to any experimental treatments using methods similar to Nuttle et al. (2013). The fence and gap treatments were applied in 2000. Fences were 2 m tall and gaps (mean ~ 250 m^2) were created by girdling trees greater than 10 cm diameter at breast height (dbh) and injecting them with herbicide (Accord)[1]. One centrally located gap was created in each subplot. Prescribed fire was applied in the spring of 2001. Strip head fires were used to control the rate of spread and fire intensity, and no overstory mortality due to fire occurred. Fire temperatures were greatest at ground surface (245 ± 15.4 °C) and coolest at 1 m from ground surface (91.9 ± 1.7 °C) as measured by fire-sensitive paints on aluminum tags (Royo et al. 2010). The prescribed fire generally simulated historic surface fire by consuming mainly leaf litter and small woody debris with most subplots experiencing nearly complete burns (Royo et al. 2010).

---

[1] Product Disclaimer: The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

Pesticide Precautionary Statement: This publication reports research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All uses of pesticides must be registered by appropriate state or federal agencies, or both, before they can be recommended. CAUTION: Pesticides can be injurious to humans, domestic animals, desirable plants, and fish or other wildlife — if they are not handled or applied properly. Use all pesticides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and pesticide containers.

Fig. 2. Generalized treatment layout for one main plot. Fire was randomly assigned to one half of the plot. Gap and fence were randomly assigned to sampling plots.



Data collection

Before treatment (1999), all individual tree stems greater than 140 cm tall were identified, mapped, tagged, and dbh measured in each plot. In the center of each plot, a 100 m² subplot was established where all seedlings greater than 20 cm in height were tagged, mapped, and measured for height and basal diameter. Seedlings were defined as those stems less than 2.54 cm in dbh and saplings as stems over 140 cm and between 2.54 and 12.7 cm dbh. Sampling of seedlings in 2007/2008 occurred on five randomly placed 0.001 ha circular plots throughout the 400 m² plot. Saplings and overstory trees were sampled on the entire 400 m² plots.

Data analysis

To test for initial site differences between the FEF and MNF, the relative abundances and importance values (IVs) of the species of concern were compared by main plot (means and variances for the 4 main plots) through PROC GLM (SAS 2006). All response variables were arcsine square-root transformed before analysis. Oak species were grouped together for analysis because low numbers of saplings were found at both sites. When statistically significant differences existed between the main sites (α = 0.05), subsequent analyses were made separately by site.

For seedlings, relative abundances (percent of total stems/ha) were calculated pre- and post-treatment (1999 and 2007/2008, respectively). For saplings, IVs were calculated as the average of the species' relative abundance (percent of total stems/ha) and relative basal area (percent of total basal area/ha in m²) for the same time periods as the seedlings.

Analyses of treatment effects and interactions were made using a generalized linear mixed model via PROC GLIMMIX using a pseudo-likelihood estimation technique (SAS 2006). A split-plot factorial repeated-measures design was used with fire as the whole plot unit and fence and gaps as the subplot units. The levels of fire (fire/no fire), canopy gap (gap/no gap), browse control (fence/no fence), and their associated interactions were modeled as fixed effects. Time was the repeated measurement in the model and the between-year correlation was evaluated with an autoregressive covariance structure. Denominator degrees of freedom were adjusted using the Kenward–Rogers method and the Tukey–Kramer method was used to adjust for multiple comparisons (Littell et al. 2006). Multiple pairwise comparisons and contrasts were made for main effects and the two-way interactions where both levels of two factors are averaged across the third factor.

The dependent variables were evaluated using the exponential distribution and the log link function. Dependent variables analyzed were relative abundances of striped maple, red maple, sugar maple, black birch, yellow-poplar, and all oak species seedlings and IVs for saplings of the same species. The GLIMMIX model was designed to detect overall differences caused by treatment (between-subject effects) and two-way interactions among treatments and time (within-subject effects). The within-subject effects are described three ways: treatments as binary (i.e., all fire treatments compared with all non-fire treatments), interactions between two treatments (i.e., fire and no fire treatments compared with gap and no gap treatments averaged across both fence and non-fence treatments), or as the eight individual treatments. The eight

Table 2. Results of repeated-measures, mixed model regression analysis on seedling relative abundance and sapling importance values; arrows (↑ or ↓) indicate the direction of main effects.

	P value							
Species size class (location)	Time	Fire × time	Fence × time	Gap × time	Fence × gap × time	Fire × fence × time	Fire × gap × time	Fire × fence × gap × time
Red maple								
Seedlings (FEF)	**<.0001↑**	**<.0001↓**	**0.0131↑**	**0.0207↑**	0.0808	0.9910	0.0590	0.1289
Seedlings (MNF)	**0.0198↑**	0.1792	0.7560	0.3101	0.1074	0.5878	0.1263	0.8537
Saplings (FEF)	**<.0001↓**	**0.0002↓**	0.3884	**0.0003↓**	**0.0149**	0.0968	**<.0001**	0.1150
Saplings (MNF)	0.1070	0.2555	0.8756	0.0770	0.4450	0.8243	0.0733	0.3063
Sugar maple								
Seedlings (FEF)	0.6467	**0.0032↓**	**0.0060↑**	0.4383	**0.0383**	0.2390	0.0664	0.5166
Seedlings (MNF)	**0.0465↑**	0.8405	**0.0062↑**	0.4657	0.0771	0.3087	0.9515	0.8629
Saplings (FEF)	**0.0192↓**	0.0533	0.5319	0.0760	0.7853	0.5727	0.5166	0.4323
Saplings (MNF)	0.09864	0.0847	0.1102	0.2903	0.3467	0.6853	0.1127	0.0726
Striped maple								
Seedlings (FEF)	**<.0001↓**	**0.0003↓**	0.2758	0.6838	0.5213	0.1263	**0.0081**	0.3436
Seedlings (MNF)	**<.0001↓**	**0.0002↓**	0.6103	0.1245	0.5420	0.5266	0.3387	0.2393
Saplings (FEF)	0.4297	**0.0275↓**	**0.0124↓**	**0.0078↑**	0.7056	0.2233	0.1004	0.4128
Saplings (MNF)	**<.0001↓**	**<.0001↓**	0.8232	**<.0001↑**	**0.0121**	0.1621	**<.0001**	0.0430
Black birch								
Seedlings	**<.0001↑**	**<.0001↑**	**<.0001↓**	**<.0001↑**	0.1759	**<.0001**	**0.0006**	0.2087
Saplings	**0.0051↑**	0.8223	**0.0003↑**	**0.0010↑**	0.1072	**0.0001**	**0.0051**	0.7843
Yellow-poplar								
Seedlings	**<.0001↑**	**<.0001↑**	0.7667	**<.0001↑**	0.8548	0.2244	**<.0001**	0.2278
Saplings	**0.0001↑**	0.2651	0.1229	**<.0001↑**	0.8847	**0.0148**	0.1373	0.3989
Oak species								
Seedlings	**0.0015↓**	0.1659	0.5194	0.9700	0.6247	0.6594	0.4903	0.6924
Saplings	0.6478	0.7066	0.1528	0.8897	**0.0004**	**0.0122**	0.4857	0.7945

Note: FEF, Fernow Experimental Forest; and MNF, Monongahela National Forest.

individual treatments are Control, Fence, Gap, Fence + Gap, Fire, Fire + Fence, Fire + Gap, and Fire + Fence + Gap. The eight individual treatments were the treatments applied at the plot level and are a method to look at the three-way interactions of fire, browse control, and canopy gaps. The naming convention for this analysis is that the eight individual treatments are capitalized; factors given in lowercase indicate that the response variable has been averaged across the two levels of the other two factors.

Results

For maple species only, we analyzed data separately between sites because all species of maples were significantly more abundant (both seedlings and saplings) at FEF than MNF prior to implementing our treatments. Except as noted, all comparisons are between post-treatment measurement periods. In the following sections, statistically significant interactions are presented first followed by significant main effects of fire, protection from browse, and canopy gaps where significant interactions were not found. Finally, means are compared as eight separate treatments as another way to view the interactions of the three processes.

Significant two-way interactions

On the FEF, browsing caused a significant decrease in sugar maple seedling relative abundance but only without canopy gaps (Table 2; Fig. 3A). The significant main effect of fire in reducing striped maple seedling abundance was greatest in the absence of canopy gaps, significantly reducing the relative abundance from ~48% (no gap, no fire) to ~9% (gap and fire) (Fig. 3B). However, the reduction in striped maple relative abundance observed with canopy gaps and fire was not significantly different from plots with no fire canopy gap (~17%). Fire and lack of browse control (unfenced plots) interact to increase black birch seedling relative abundance 2-fold relative to fire or browse control (Fig. 3C). Gaps and fire together caused the relative abundance of black birch to increase from 0% to 10% over gap alone (Fig. 3D). Since the differences between fire and no gap, fire and gap, and no fire and no gap are not statistically significant, this interaction is a representation of the significant main effects of fire and gaps on the increase in relative abundance of black birch seedlings. Gaps and fire together caused a 12% increase in the relative abundance of yellow-poplar versus gap alone (Fig. 3E).

Fire and gaps together decreased red maple sapling IVs (Fig. 4A) to zero. The main effect of fire in reducing striped maple IVs on MNF plots was greatest when fire occurred in plots with no canopy gaps created (Fig. 4B). Fire and canopy gaps increased black birch sapling IVs but the increase was only significant when compared with plots with fire but no canopy gaps (Fig. 4C). Excluding browsers increased the IV of black birch but to a much lesser degree following fire (significant fire × browsing interaction; Fig. 4D). Neither fire nor excluding browsers alone caused any significant change in the IVs of yellow-poplar; however, together they resulted in significantly greater yellow-poplar IVs than browse control alone (Fig. 4E). Canopy gaps and the exclusion of browsers together nearly doubled oak sapling IVs versus either treatment alone; however, IVs for all oak species remained low (Fig. 4F).

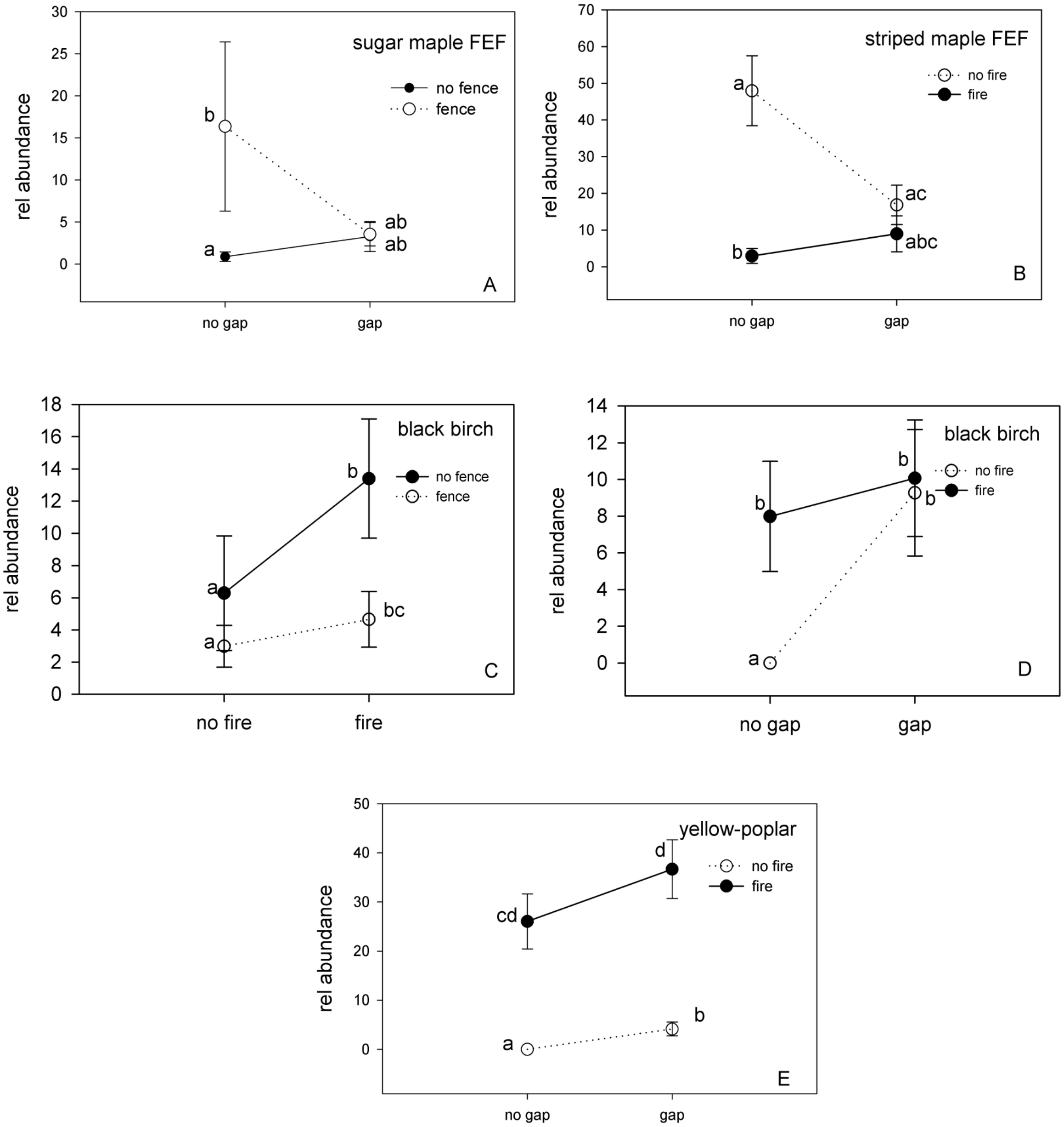
Significant main effects

Regardless of the presence or absence of canopy gaps or fences, fire caused significant reductions of red maple seedlings (FEF plots), sugar maple seedlings (FEF plots), and striped maple seedlings and saplings (MNF plots) (Table 3). Fire decreased the relative abundance of red maple 10-fold (fire = 1%; no fire = 11%) and reduced red maple sapling IVs by half (fire = 8%; no fire = 16%). Fire also reduced striped maple IVs by 13% (MNF).

Browsing decreased sugar maple seedling relative abundances (Table 3) from 2.4% to ~0.2% on the MNF plots regardless of the presence or absence of gaps or fire. On the FEF plots, browsing significantly reduced red maple seedling relative abundances from 8% to 5%. Excluding browsers significantly decreased the mean IV of striped maple saplings (FEF plots) from 18% to ~10%.

Canopy gaps significantly increased red maple seedling relative abundance from 1.2% to ~7% (FEF plots). Gaps caused a nearly 20%

Fig. 3. Significant (α = 0.05) two-way interactions for mean seedling relative abundance of the following selected species: (A) sugar maple, (B) striped maple, (C) and (D) black birch, and (E) yellow-poplar. All comparisons are made for the post-treatment time period only. Means (±SE) are calculated across the third treatment factor; means with the same letter are not significantly different. FEF, Fernow Experimental Forest.



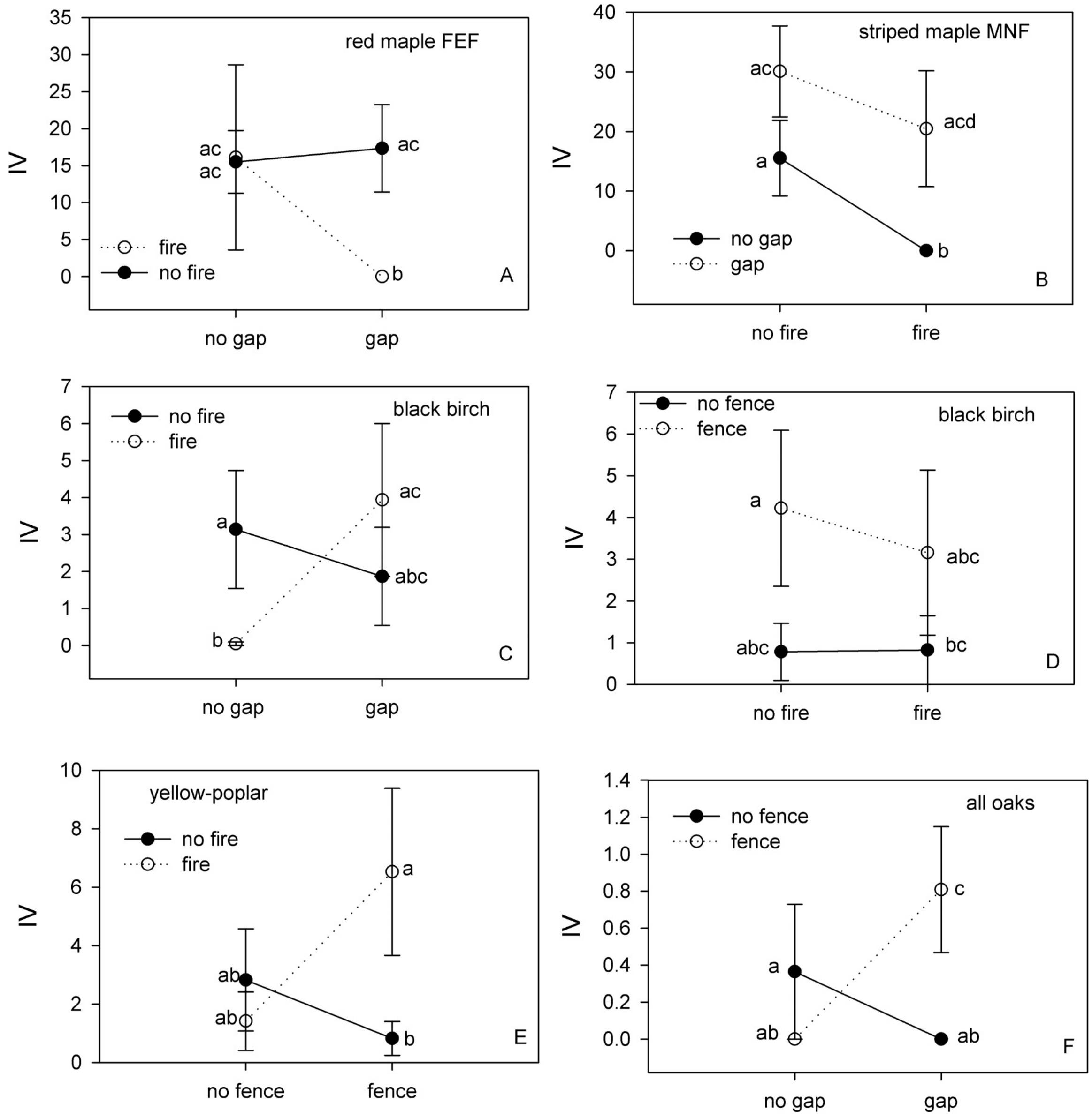
increase in striped maple sapling IVs on FEF plots (gaps = 25%; no gap = 4%). Gaps increased the IV of yellow-poplar from about 1% without gaps to 5% with gaps (Table 3).

Significant effects of the eight treatments

On the FEF plots, striped maple relative abundance was lowest on the Fire plots and was significantly different from all other treatments except Fire + Fence and Fire + Gap (Fig. 5C). On the MNF plots, the Fire + Fence + Gap treatment resulted in significantly lower abundances than the Control, Fence, and Gap treatments and had the lowest relative abundance of striped maple (Fig. 5D). The Fire + Gap treatment had the lowest abundance of red maple post-treatment for the FEF plots, and this treatment effect was significantly different from all the treatments without fire (Fig. 5E). For the MNF plots, there were no statistically significant differences among treatments for relative abundances of red maple seedlings (Fig. 5F), likely because of the high variability observed post-treatment; the same is true for red maple sapling IVs (Fig. 7E and 7F). Black birch relative abundance was greatest in the Fire + Gap treatment, although this value was statistically different only from the Control and Fence treatments (Fig. 6A). Similarly, yellow-poplar responded to disturbance with all relative abundances in fire treatments statistically the same and significantly different from those treatments without fire (Fig. 6B). No treatment resulted in significant differences in mean relative abundance values for the oak species (Fig. 6C).

When compared post-treatment, Fire and Fire + Fence treatments resulted in the lowest striped maple IVs, and these values were significantly different from the Gap and Fire + Gap treatments for the FEF plots (Fig. 7C). For the MNF plots, Fire and Fire + Fence treatments also resulted in the lowest striped maple IVs, and values for these treatments were significantly different from all other treatments (Fig. 7D). The Fire treatment resulted in the

Fig. 4. Significant (α = 0.05) two-way interactions for mean sapling importance values (IV) of the following selected species: (A) red maple, (B) striped maple, (C) and (D) black birch, (E) yellow-poplar, and (F) all oaks. All comparisons are made for the post-treatment time period only. Means (±SE) are calculated across the third treatment factor; means with the same letter are not significantly different. FEF, Fernow Experimental Forest; and MNF, Monongahela National Forest.



lowest black birch sapling IV, which differed significantly from the Fire + Fence + Gap and Fence treatments (Fig. 8A). Fire and browse control together increased yellow-poplar sapling IVs above browse control alone (Fig. 8B). The Fire treatment resulted in the lowest yellow-poplar IV post-treatment, and this mean value was significantly different from only the Fire + Fence + Gap treatment (Fig. 8B). There were no significant differences among treatments for oak saplings (Fig. 8C).

Discussion

Fire reduced the abundance and IVs of red maple and striped maple but sugar maple was not as affected with only seedling abundance on FEF plots reduced in response to fire. These reductions were expected given the fire sensitive nature of maple species and similar results of a near-by study (Schuler et al. 2013). In our study, this reduction in maple abundance and IVs is still noticeable 7–8 years after fire. One prescribed fire increased the IVs and relative abundances of yellow-poplar saplings and seedlings despite yellow-poplar being considered fire sensitive (Beck 1990). This serves as a reminder that species are adapted to a disturbance regime (Keeley et al. 2011) — the combination of intensity, severity, and periodicity — and provides support for conducting another prescribed fire in this long-term study.

Our results are not straightforward with some species and size classes increasing with browse control and others decreasing in relative abundance or IV. As found for the herbaceous layer (Royo et al. 2010), interactions among fire, browse control, and gaps were common. Royo et al. (2010) demonstrated that gaps and fire increased species richness, cover, and diversity of herbaceous species. However, in our study, the individual species assessed differed in their response to the three processes making it difficult to determine one trend. While interactions were common in our study, we found just two species/size combinations where main effects were not statistically significant but an interaction of two

Table 3. Mean (SE) seedling relative abundances and sapling importance values at the 2007/2008 measurement period summarized by main treatment factor (i.e., fire/no fire means are averaged across both levels of the other two factors).

Species size class (location)	Fire (%)	No fire (%)	Fence (%)	No fence (%)	Gap (%)	No gap (%)
Red maple						
Seedlings (FEF)	0.8 (0.006)	11.3 (0.03)	8.2 (0.03)	3.9 (0.01)	6.8 (0.02)	5.3 (0.03)
Seedlings (MNF)	3.9 (0.01)	10.4 (0.02)	8.2 (0.02)	6.0 (0.02)	7.9 (0.02)	6.3 (0.02)
Saplings (FEF)	8.0 (0.06)	16.4 (0.04)	7.6 (0.03)	16.9 (0.06)	8.7 (0.04)	15.8 (0.06)
Saplings (MNF)	21.4 (0.07)	34.7 (0.06)	28.6 (0.06)	27.5 (0.07)	18.6 (0.04)	37.5 (0.08)
Sugar maple						
Seedlings (FEF)	6.5 (0.05)	5.5 (0.02)	10.0 (0.05)	2.1 (0.01)	3.4 (0.01)	8.6 (0.05)
Seedlings (MNF)	0.5 (0.003)	2.2 (0.009)	2.4 (0.009)	0.25 (0.002)	1.5 (0.009)	1.6 (0.005)
Saplings (FEF)	42.0 (0.11)	42.5 (0.06)	40.8 (0.08)	43.8 (0.09)	28.0 (0.07)	56.5 (0.09)
Saplings (MNF)	13.2 (0.07)	10.3 (0.02)	11.4 (0.06)	12.1 (0.05)	6.5 (0.02)	17.0 (0.07)
Striped maple						
Seedlings (FEF)	6.0 (0.03)	32.4 (0.07)	21.9 (0.06)	16.4 (0.06)	12.9 (0.04)	25.4 (0.07)
Seedlings (MNF)	18.2 (0.03)	46.9 (0.08)	28.0 (0.07)	37.1 (0.06)	25.1 (0.06)	40.0 (0.07)
Saplings (FEF)	12.4 (0.08)	16.3 (0.05)	10.6 (0.05)	18.1 (0.07)	24.7 (0.08)	4.1 (0.03)
Saplings (MNF)	10.2 (0.05)	22.8 (0.05)	11.2 (0.04)	21.8 (0.06)	25.3 (0.06)	7.8 (0.04)
Black birch						
Seedlings	9.0 (0.02)	4.6 (0.02)	3.9 (0.01)	9.8 (0.03)	8.6 (0.02)	5.0 (0.02)
Saplings	2.0 (0.01)	2.5 (0.01)	3.7 (0.01)	0.80 (0.005)	2.9 (0.01)	1.6 (0.008)
Yellow-poplar						
Seedlings	31.4 (0.04)	2.1 (0.008)	16.1 (0.04)	17.3 (0.04)	20.1 (0.04)	13.2 (0.04)
Saplings	4.0 (0.01)	1.8 (0.01)	3.7 (0.01)	2.1 (0.01)	4.6 (0.02)	1.2 (0.007)
Oak species						
Seedlings	9.1 (0.03)	10.5 (0.02)	9.1 (0.02)	10.5 (0.03)	9.9 (0.02)	9.7 (0.03)
Saplings	0.2 (0.001)	0.4 (0.002)	0.4 (0.002)	0.2 (0.002)	0.40 (0.002)	0.18 (0.002)

Note: FEF, Fernow Experimental Forest; and MNF, Monongahela National Forest.

factors was significant for post-treatment means. In both instances, browse control is significant in the interaction (fire and fence increased the IVs of yellow-poplar saplings and fence and gaps increased the IVs of oak saplings). This would suggest that controlling browse is necessary for these disturbance-dependent tree species to respond as expected. As a shade-intolerant species that responds to disturbances, the increases in yellow-poplar we document may be due to prescribed fire removing leaf litter and favoring germination of abundant yellow-poplar seed (Glasgow and Matlack 2007).

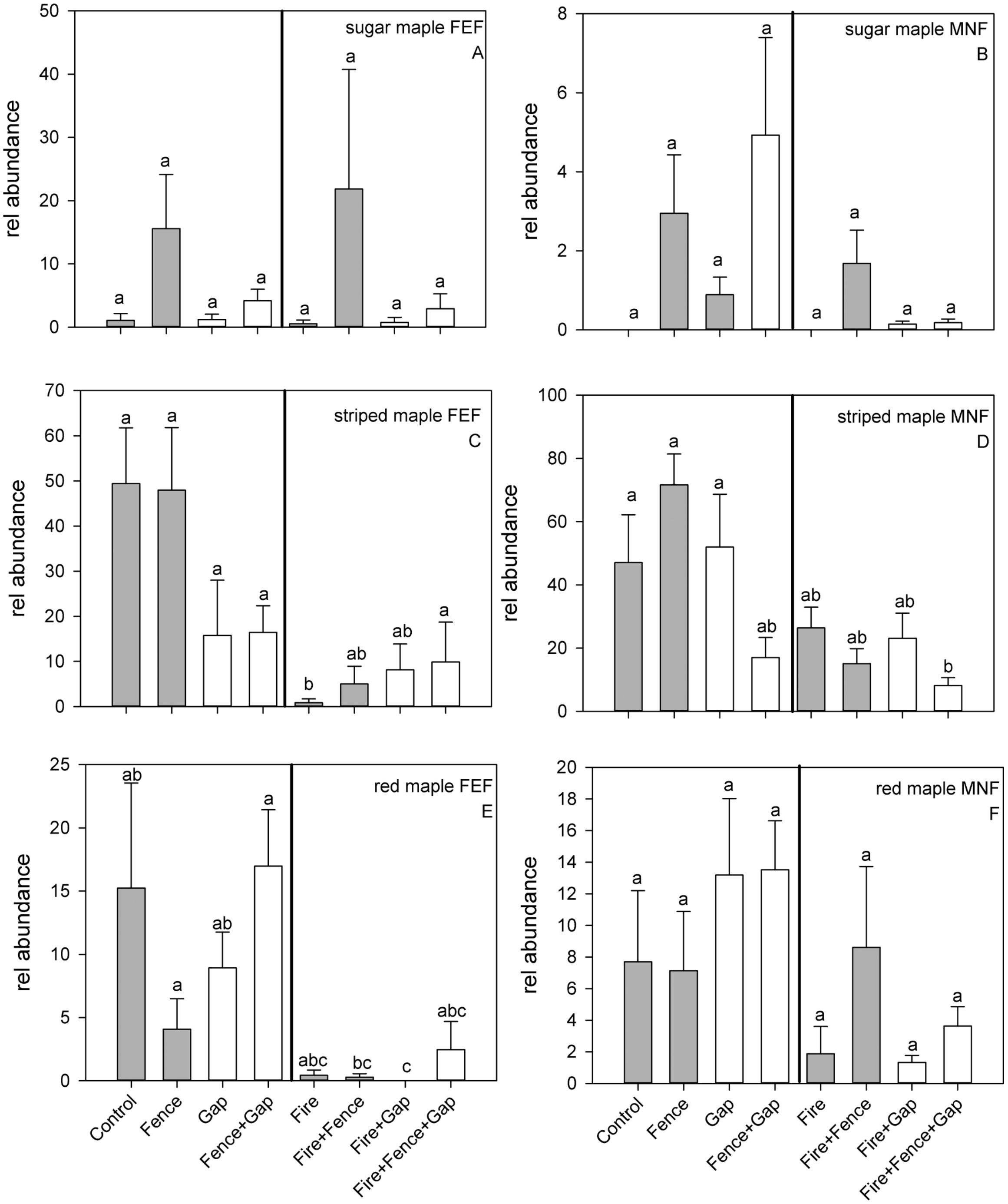
Given their shade tolerances, we expected that yellow-poplar, black birch, and oaks would increase in relative abundance and IV in those areas with canopy gaps. When we excluded deer and created gaps, oak saplings increased in IV in both the presence and absence of fire when compared with areas with no gaps and browsing allowed. This suggests that with reduced browsing pressure and large canopy disturbances typical of old-growth forests, oaks can remain in the community, although IVs were still low for oak species. Fire, browse control, nor canopy gaps alone or in combination increased the seedling relative abundance of oak species although one prescribed fire did reduce the relative abundance of maple seedlings. Recent synthesis work on the ecology and silviculture of oak species includes the recommendation that multiple fires may be necessary to benefit oak species over maples (Johnson et al. 2009; Dey et al. 2010; Brose et al. 2013).

Fire suppression, smaller canopy gaps due to smaller tree canopies in second-growth forests, and browsing have created forest understories that are dominated by a small number of tree species that are simultaneously browse tolerant, fire sensitive, and shade tolerant (Nuttle et al. 2013). Indeed, at our two study sites, the seedling and sapling layer were dominated by maple species (Table 1). While the composition of the maple species varied by site, at the FEF maples comprised 55% of the seedling layer and ~76% of the sapling layer. At the MNF maples comprised ~46% of the seedling layer and ~66% of the sapling layer (estimates at both sites based on stems/ha). In contrast, oak seedlings made up approximately 24% (FEF site) or 25% (MNF site) of the seedling layer and less than 1% (FEF site) and ~1% (MNF site) of the sapling layer before the study began. Given this legacy understory, it is not surprising that our results show that interactions among the three key processes were common for many species and both size classes and that the single prescribed fire did not increase the relative abundance or IV of oak species already at low abundance at the start of the study. However, in a study adjacent to our FEF plots, after two prescribed fires, oak seedling abundance was about equal to maples and yellow-poplar based on stems per acre (Schuler et al. 2013). Prescribed fire is expected to be applied again to the study area in the future, and we will be able to determine the effects of repeated burning.

Although the presence of browse-sensitive species such as sugar maple in both sites, as both seedlings and saplings, would suggest that deer browse pressure has not been at high levels compared with other areas, experimental browse control did show a positive effect especially in combination with other factors. This demonstrates the legacy effect of browse. Royo et al. (2010) demonstrated that gaps and fire increased species richness, cover, and diversity of herbaceous species. In our plots where fire and gaps occurred and deer browse was excluded (Fire + Fence + Gap), the herbaceous layer was dominated by blackberry (*Rubus allegheniensis* Porter), a shrub highly palatable to deer. With deer browsing, the percentage cover of this shrub was reduced, resulting in increased overall herbaceous richness. Deer browsing and dominance of blackberry were hypothesized as causes for reduced tree regeneration and the magnitude of response to increasing gap size 12 years after partial harvest (Kern et al. 2012); although after overstory removal, tree regeneration likely emerges above blackberry 5 to 7 years postharvest (see Donoso and Nyland 2006 for review).

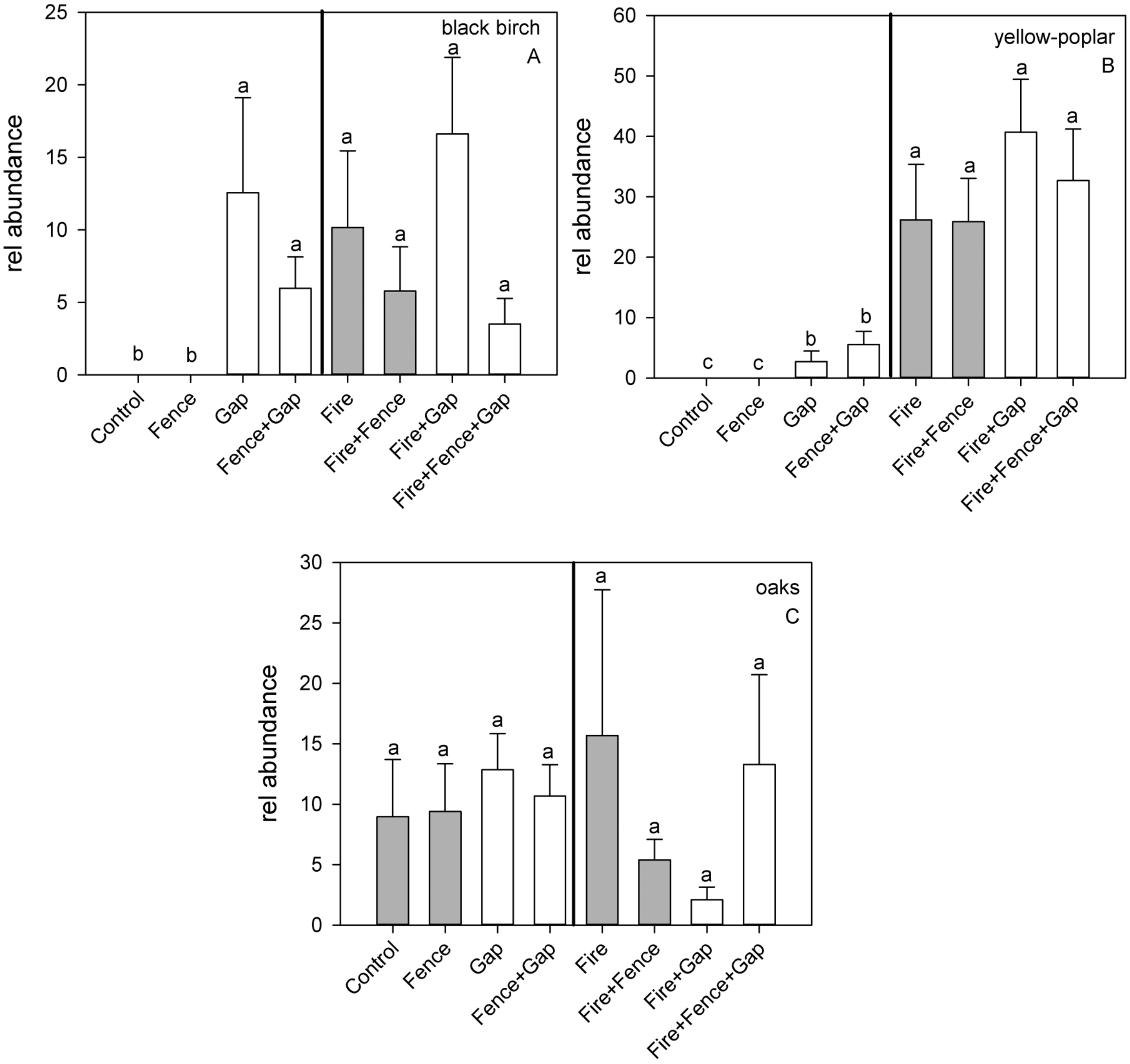
Differing regeneration strategies between oaks species and potential competitors set the stage for management difficulties in regenerating oak species. Although thinning and prescribed fire can create canopy recruitment opportunities, in a study in Ohio maples captured these opportunities and oak recruitment was minimal (Chiang et al. 2008), and while oaks made up half the gap-makers in natural gaps in second-growth forests, 43% of the

Fig. 5. Mean seedling relative abundance (±SE) of maple species by treatment. (A) and (B) Sugar maple, (C) and (D) striped maple, and (E) and (F) red maple. Means with the same letter are not significantly different (α = 0.05). Open bars are those treatments that include canopy gaps; the vertical line separates non-fire from fire treatments. FEF, Fernow Experimental Forest; and MNF, Monongahela National Forest.



species in canopy gaps were maples (Hart and Grissino-Mayer 2009). Oak species are generally considered moderately shade intolerant and oak regeneration is usually more abundant in gaps formed by multiple trees compared with single-tree gaps (Clinton et al. 1994). Oaks rely on a bud bank instead of a seed bank for creating seedling sprouts able to ascend to the forest canopy after a disturbance (see reviews in Johnson 1993; Johnson et al. 2009; Dey et al. 2010), and the shoot portion of a seedling sprout may be decades younger than the root system (Merz and Boyce 1956; Tryon and Powell 1984; Heggenstaller et al. 2012). In contrast, black birch and yellow-poplar rely on different regeneration strategies than oak species, ones that do not include the development of seedling sprouts resulting from dieback and resprouting (Crow 1988). Advance regeneration of oak is generally a mix of true seedlings and seedling sprouts with stump sprouts also contributing to the oak regeneration potential of a site (Beck 1970; Sander and Clark 1971; Sander 1972; McQuilkin 1975; Johnson 1993); however, seedling sprouts are often the majority of regeneration found under a closed-canopy forest (Crow 1988). Yellow-poplar seeds retain viability in the forest floor for 4 to 7 years (Beck 1990),

Fig. 6. Mean seedling relative abundance (±SE) of (A) black birch, (B) yellow-poplar, and (C) oak species by treatment. Means with the same letter are not significantly different (α = 0.05). Open bars are those treatments that include canopy gaps; the vertical line separates non-fire from fire treatments.



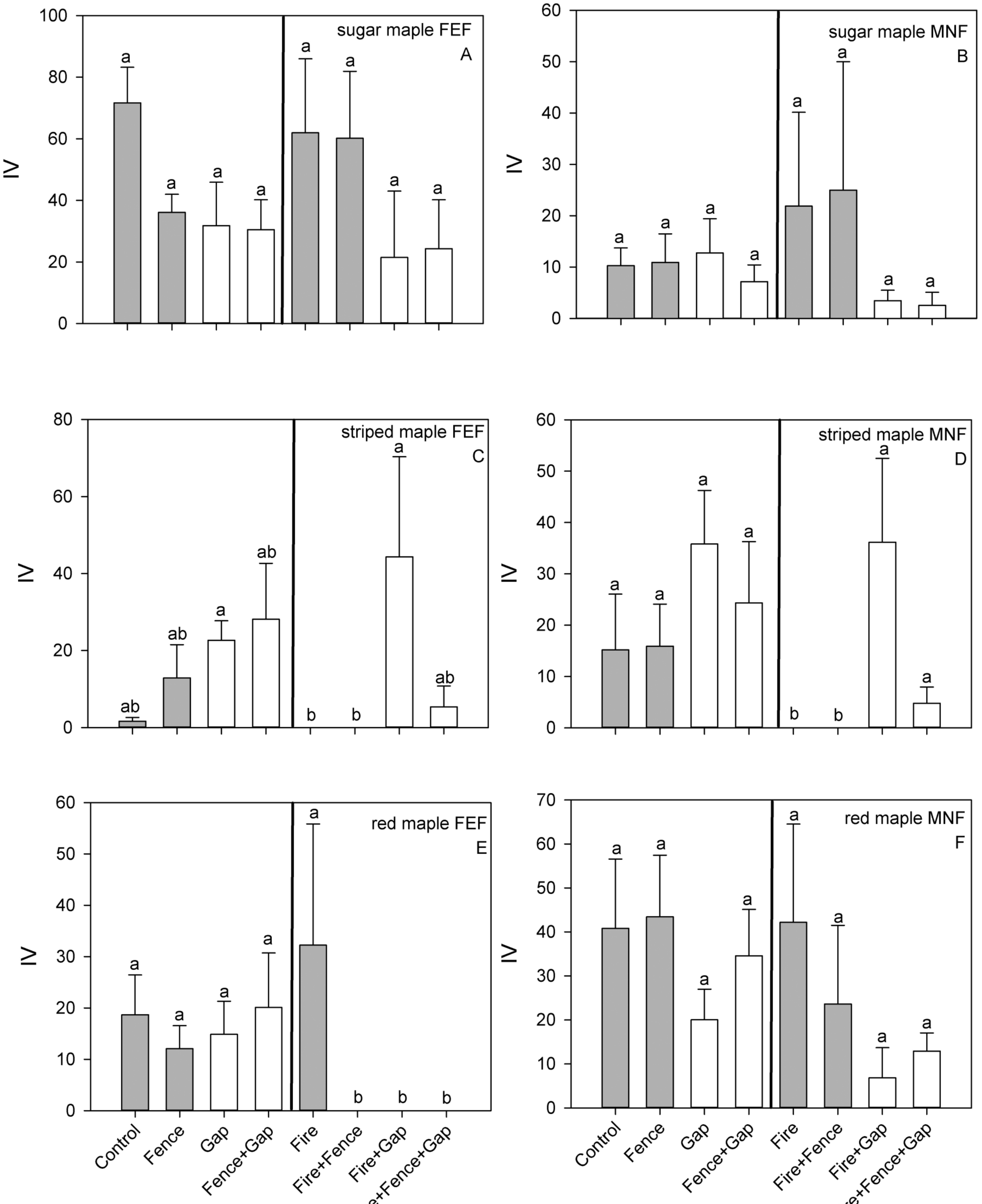
and birch seeds have been found to retain viability for more than a year while chestnut oak and Northern red oak were not found in the soil seed bank in the southern Appalachian Mountains (Hille Ris Lambers et al. 2005).

Although the study area has been accumulating oak seedlings (Table 1), success of advance regeneration after overstory removal depends on the size of advance regeneration not just numbers of stems (Sander 1971). However, we observed an increase in oak sapling IVs in areas with browse control and canopy gaps over other treatments. Even though oak sapling IVs did not increase between pre- and post-treatment and oaks remained a small proportion of the sapling layer, controlling browse through fencing or reducing the deer population should be considered when oak regeneration is desired and canopy gaps are planned.

While this study was not specifically designed to test a silvicultural treatment or set of treatments to reverse the conversion of oak-dominated stands to more mesic species, the results can inform land managers' and foresters' efforts to control species composition. For land managers using prescribed fire to restore a historic disturbance regime that is favorable to oak-dominated forests, our results show that a single prescribed fire can reduce relative abundances of maple seedlings but it also reduces oak seedling abundance. However, as others have demonstrated (Alexander et al. 2008; Wood 2010), one fire is generally not sufficient to reverse decades of fire suppression and this is even more likely in mesic areas (Iverson et al. 2008). The slow change in site conditions associated with the cessation of periodic fire is a positive feedback system whereby the exclusion of fire encourages the growth of shade-tolerant mesophytic hardwoods instead of oak (Nowacki and Abrams 2008). As mesophytic species increase, the system becomes less fire-prone with dense shade and moist, cool microclimates and fuels that are less conducive to burning (Nowacki and Abrams 2008). Schuler et al. (2010) have further emphasized the importance of black birch and yellow-poplar in the seed bank as a barrier to oak restoration. Thus, one fire event may not reverse the slow creation of a shade-tolerant and fire-sensitive understory after decades of fire suppression and may not yield enough information to answer our original question on the effects of prescribed fire on oak regeneration in a mesic forest.

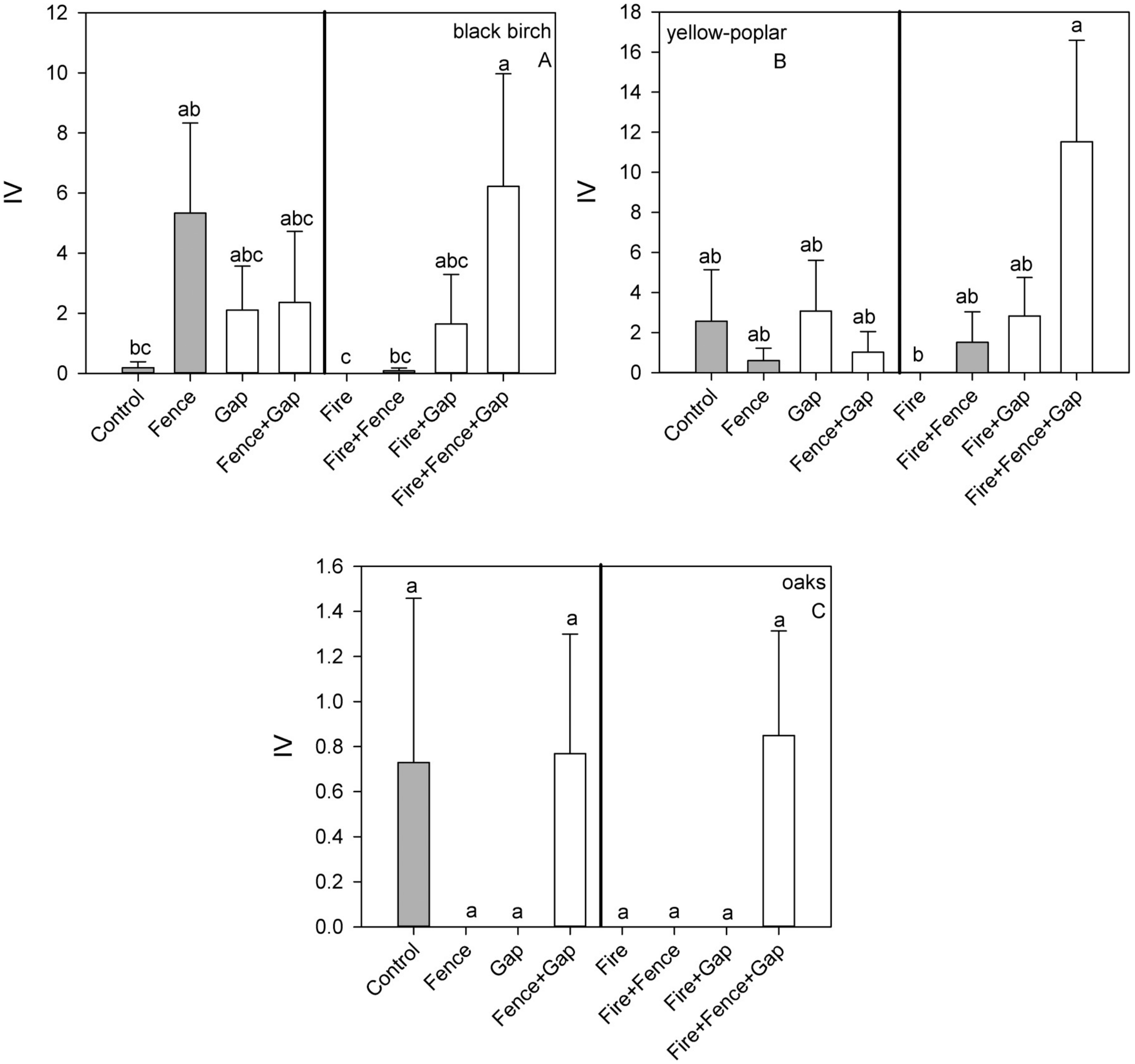
In addition to the frequency of disturbance, controlling the timing of interacting disturbance events may be a missing element in the current study. Silvicultural prescriptions for regenerating

Fig. 7. Mean sapling importance values (IV; ±SE) of maple species by treatment. (A) and (B) Sugar maple, (C) and (D) striped maple, and (E) and (F) red maple. Means with the same letter are not significantly different (α = 0.05). Open bars are those treatments that include canopy gaps; the vertical line separates non-fire from fire treatments. FEF, Fernow Experimental Forest; and MNF, Monongahela National Forest.



oak-dominated forests recommend overstory reduction or removal only after interfering vegetation has been removed or reduced, often through fire or herbicide (Brose et al. 2008; Johnson et al. 2009). Hutchinson et al. (2012) reported that oaks were more abundant in canopy gaps formed after repeated fires had removed shade-tolerant species. In the current study, canopy gaps were initiated just before prescribed fire with the release of growing space and disturbance to forest floor coincident with the dieback and sprouting of existing oak advance regeneration. These coincident disturbances created conditions where oak seedling sprouts likely faced the maximum pressure from other vegetation, based on stem densities. Our results highlight the need for further study of the timing of combined disturbances to develop silvicultural prescriptions to perpetuate oaks in oak-dominated forests undergoing successional replacement by shade-tolerant, fire-sensitive species. We will continue to monitor the stand dynamics of this study and additional prescribed burns are possible. We expect that as the canopy gaps close and short-lived gap-filling

Fig. 8. Mean sapling importance values (IV; ±SE) of (A) black birch, (B) yellow-poplar, and (C) oak species by treatment. Means with the same letter are not significantly different ($\alpha = 0.05$). Open bars are those treatments that include canopy gaps; the vertical line separates non-fire from fire treatments.



species decline, some differences among treatments documented here may change.

Acknowledgements

Funding for this study (4300-FS-NE-4353-13) has come from the University of Pittsburgh, USDA Forest Service Northern Research Station, and USDA National Research Initiative Competitive Grant 99-35101-7732 to Walter Carson. We are grateful to Rachel Collins for setting up this study and to all the assistants who collected data over the years of this study. We thank two anonymous reviewers whose comments helped clarify the results and improve the manuscript.

References

Abrams, M.D. 1990. Adaptations and responses to drought in Quercus species of North America. Tree Physiol. **7**: 227–238. doi:10.1093/treephys/7.1-2-3-4.227.

Abrams, M.D. 1992. Fire and the development of oaks. BioScience, **42**(5): 346–353. doi:10.2307/1311781.

Abrams, M.D., and Downs, J.A. 1990. Successional replacement of old-growth white oak by mixed mesophytic hardwoods in southwestern Pennsylvania. Can. J. For. Res. **20**(12): 1864–1870. doi:10.1139/x90-250.

Adams, M.B., Burger, J., Zelazny, L., and Baumgras, J. 2004. Description of the Fork Mountain long-term soil productivity study: site characterization. USDA Forest Service General Technical Report NE-323.

Albrecht, M.A., and McCarthy, B.C. 2006. Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests. For. Ecol. Manage. **226**: 88–103. doi:10.1016/j.foreco.2005.12.061.

Alexander, H.D., Arthur, M.A., Loftis, D.L., and Green, S.R. 2008. Survival and growth of upland oak and co-occurring competitor seedlings following single and repeated prescribed fires. For. Ecol. Manage. **256**: 1021–1030. doi:10.1016/j.foreco.2008.06.004.

Arthur, M.A., Paratley, R.D., and Blankenship, B.A. 1998. Single and repeated fires affect survival and regeneration of woody and herbaceous species in an oak-pine forest. J. Torrey Bot. Soc. **125**(3): 225–236. doi:10.2307/2997220.

Barnes, T.A., and Van Lear, D.H. 1998. Prescribed fire effects on advanced regeneration in mixed hardwood stands. South. J. Appl. For. **22**(3): 138–142.

Beck, D.E. 1970. Effect of competition on survival and height growth of red oak seedlings. USDA Forest Service Research Paper SE-56, Southeastern Forest Experiment Station, Asheville, NC.

Beck, D.E. 1990. Yellow-poplar. *In* Silvics of North America: 1. Conifers; 2. Hardwoods. *Edited by* R.M. Burns and B.H. Honkala (*technical coordinators*). Agriculture Handbook 654. USDA Forest Service, Washington, DC.

Blankenship, B.A., and Arthur, M.A. 2006. Stand structure over 9 years in burned and fire-excluded oak stands on the Cumberland Plateau, Kentucky. For. Ecol. Manage. **225**: 134–145. doi:10.1016/j.foreco.2005.12.032.

Brashears, M.B., Fajvan, M.A., and Schuler, T.M. 2004. An assessment of canopy stratification and tree species diversity following clearcutting in central Appalachian hardwoods. For. Sci. **50**(1): 54–64.

Brose, P.H. 2010. Long-term effects of single prescribed fires on hardwood regeneration in oak shelterwood stands. For. Ecol. Manage. **260**: 1516–1524. doi:10.1016/j.foreco.2010.07.050.

Brose, P.H., and Van Lear, D.H. 1998. Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. Can. J. For. Res. **28**(3): 331–339. doi:10.1139/x97-218.

Brose, P.H., Gottschalk, K.W., Horsley, S.B., Knopp, P.D., Kochenderfer, J.N., McGuinness, B.J., Miller, G.W., Ristau, T.E., Stoleson, S.H., and Stout, S.L. 2008. Prescribing regeneration treatments for mixed-oak forests in the Mid-Atlantic region. USDA Forest Service General Technical Report NRS-33.

Brose, P.H., Dey, D.C., Phillips, R.J., and Waldrop, T.A. 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.

Campbell., T.A., Laseter, B.R., Ford, W.M., and Miller, K.V. 2004. Feasibility of localized management to control white-tailed deer in forest regeneration areas. Wild. Soc. Bull. **32**(4): 1124–1131. doi:10.2193/0091-7648(2004)032[1124:FOLMTC]2.0.CO;2.

Canham, C.D., Finzi, A.C., Pacala, S.W., and Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Can. J. For. Res. **24**(2): 337–349. doi:10.1139/x94-046.

Chiang, J.-M., McEwan, R.W., Yaussy, D.A., and Brown, K.J. 2008. The effects of prescribed fire and silvicultural thinning on the aboveground carbon stocks and net primary production of overstory trees in an oak-hickory ecosystem in southern Ohio. For. Ecol. Manage. **255**: 1584–1594. doi:10.1016/j.foreco.2007.11.016.

Clebsch, E.E.C., and Busing, R.T. 1989. Secondary succession, gap dynamics, and community structure in a southern Appalachian cove forest. Ecology, **70**(3): 728–735. doi:10.2307/1940223.

Cleland, D.T., Freeouf, J.A., Keys, J.E., Jr., Nowacki, G.J., Carpenter, C., and McNab, W.H. 2007. Ecological Subregions: Sections and Subsections of the Conterminous United States [1:3,500,000] [CD-ROM]. Sloan, A.M., cartog. USDA Forest Service General Technical Report WO-76.

Clinton, B.D., Boring, L.R., and Swank, W.T. 1994. Regeneration patterns in canopy gaps of mixed-oak forests of the southern Appalachians: Influences of topographic position and evergreen understory. Am. Mid. Nat. **132**: 308–319. doi:10.2307/2426587.

Collins, R.J., and Carson, W.P. 2003. The fire and oak hypothesis: incorporating the effects of deer browsing and canopy gaps. *In* Proceedings of the 13th Central Hardwood Forest Conference. Urbana-Champaign IL April 1–3 2003. St. Paul, MN: USDA Forest Service North Central Research Station General Technical Report NC-234: 44–63.

Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., and Waller, D.M. 2004. Ecological impacts of deer overabundance. Annu. Rev. Ecol. Evol. Syst. **35**: 113–147. doi:10.1146/annurev.ecolsys.35.021103.105725.

Cowell, C.M., Hoalst-Pullen, N., and Jackson, M.T. 2010. The limited role of canopy gaps in the successional dynamics of a mature mixed *Quercus* forest remnant. J. Veg. Sci. **21**: 201–212. doi:10.1111/j.1654-1103.2009.01137.x.

Crow, T.R. 1988. Reproductive mode and mechanism for self-replacement of northern red oak (*Quercus rubra*) – a review. For. Sci. **34**: 19–40.

Davis, M.B. 1981. Quaternary history and the stability of forest communities. *In* Forest Succession: Concepts and Application. *Edited by* D.C. West, H.H. Shugart, and D.B. Botkin. Springer-Verlag, New York. pp. 132–153.

Dey, D.C., Royo, A.A., Brose, P.H., Hutchinson, T.F., Spetich, M.A., and Stoleson, S.H. 2010. An ecologically based approach to oak silviculture: A synthesis of 50 years of oak ecosystem research in North America. Revista Colombia Forestal, **13**(2): 200–222.

Dietze, M.C., and Clark, J.S. 2008. Changing the gap dynamics paradigm: Vegetation regeneration control on forest response to disturbance. Ecol. Monogr. **78**(3): 331–347. doi:10.1890/07-0271.1.

Donoso, P.J., and Nyland, R.D. 2006. Interference to hardwood regeneration in northeastern North America: The effects of raspberries (*Rubus* spp.) following clearcutting and shelterwood methods. North. J. Appl. For. **23**(4): 288–296.

Fei, S., and Steiner, K.C. 2007. Evidence for increasing red maple abundance in the eastern United States. For. Sci. **53**(4): 473–477.

Fei, S., Kong, N., Steiner, K.C., Moser, W.K., and Steiner, E.B. 2011. Change in oak abundance in the eastern United States from 1980 to 2008. For. Ecol. Manage. **262**: 1370–1377. doi:10.1016/j.foreco.2011.06.030.

Galbraith, S.L., and Martin, W.H. 2005. Three decades of overstory and species change in a mixed mesophytic forest in eastern Kentucky. Castanea, **70**: 115–128. doi:10.2179/0008-7475(2005)070[0115:TDOOAS]2.0.CO;2.

Glasgow, L.S., and Matlack, G.R. 2007. Prescribed burning and understory composition in a temperate deciduous forest, Ohio, U.S.A. For. Ecol. Manage. **238**: 54–64. doi:10.1016/j.foreco.2006.08.344.

Green, S.R., Arthur, M.A., and Blankenship, B.A. 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. doi:10.1016/j.foreco.2010.02.026.

Harmon, M.E. 1984. Survival of trees after low-intensity surface fires in Great Smoky Mountains National Park. Ecology, **65**(3): 796–802. doi:10.2307/1938052.

Hart, J.L., and Grissino-Mayer, H.D. 2009. Gap-scale disturbance processes in secondary hardwood stands on the Cumberland Plateau, Tennessee, U.S.A. Plant Ecol. **201**: 131–146. doi:10.1007/s11258-008-9488-9.

Heggenstaller, D.J., Zenner, E.K., Brose, P.H., and Peck, J.E. 2012. How much older are Appalachian oaks below-ground than above-ground? North. J. Appl. For. **29**(3): 155–157. doi:10.5849/njaf.12-008.

Hille Ris Lambers, J., Clark, J.S., and Lavine, M. 2005. Implications of seed banking for recruitment of southern Appalachian woody species. Ecology, **86**(1): 85–95. doi:10.1890/03-0685.

Hinckley, T.M., Teskey, R.O., Duhme, F., and Richter, H. 1981. Temperate hardwood forests. *In* Water Deficits and Plant Growth. *Edited by* T.T. Kozolowski. Academic Press, NY, pp. 153–208.

Horsley, S.B., Stout, S.L., and DeCalesta, D.S. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecol. Appl. **13**(1): 98–118. doi:10.1890/1051-0761(2003)013[0098:WTDIOT]2.0.CO;2.

Huddle, J.A., and Pallardy, S.G. 1999. Effect of fire on survival and growth of *Acer rubrum* and *Quercus* seedlings. For. Ecol. Manage. **118**: 49–56. doi:10.1016/S0378-1127(98)00485-X.

Hutchinson, T.F., Sutherland, E.K., and Yaussy, D.A. 2005. Effects of repeated prescribed fires on the structure, composition, and regeneration of mixed-oak forests in Ohio. For. Ecol. Manage. **218**: 210–228. doi:10.1016/j.foreco.2005.07.011.

Hutchinson, T.F., Long, R.P., Rebbeck, J., Sutherland, E.K., and Yaussy, D.A. 2012. Repeated prescribed fires alter gap-phase regeneration in mixed-oak forests. Can. J. For. Res. **42**(2): 303–314. doi:10.1139/x11-184.

Iverson, L.R., Hutchinson, T.F., Prasad, A.M., and Peters, M.P. 2008. Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern US: 7-year results. For. Ecol. Manage. **255**: 3035–3050. doi:10.1016/j.foreco.2007.09.088.

Johnson, P.S. 1993. Perspectives on the ecology and silviculture of oak-dominated forests in the central and eastern states. USDA Forest Service General Technical Report NC-153.

Johnson, P.S., Shifely, S.R., and Rogers, R. 2009. The Ecology and Silviculture of Oaks, 2nd ed. Wallingford, UK: CABI Publishing.

Kain, M., Battaglia, L., Royo, A., and Carson, W.P. 2011. Over-browsing in Pennsylvania creates a depauperate forest dominated by an understory tree: results from a 60-year-old deer exclosure. J. Torrey Bot. Soc. **138**(3): 322–326. doi:10.3159/TORREY-D-11-00018.1.

Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J., and Bradstock, R.A. 2011. Fire as an evolutionary pressure shaping plant traits. Trends Plant Sci. **16**: 406–411. doi:10.1016/j.tplants.2011.04.002.

Kern, C.C., Reich, P.B., Montgomery, R.A., and Strong, T.F. 2012. Do deer and shrubs override canopy gap size effects on growth ad survival of yellow birch, northern red oak, eastern white pine, and eastern hemlock seedlings? For. Ecol. Manage. **267**: 134–143. doi:10.1016/j.foreco.2011.12.002.

Krueger, L.M., Peterson, C.J., Royo, A., and Carson, W.P. 2009. Evaluating relationships among tree growth rate, shade tolerance, and browse tolerance following disturbance in an eastern deciduous forest. Can. J. For. Res. **39**(12): 2460–2469. doi:10.1139/X09-155.

Littell. R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., and Schabenberger, O. 2006. SAS for Mixed Models, 2nd ed. Cary, NC: SAS Institute, Inc.

Loftis, D.L. 1990. A shelterwood method for regenerating red oak in the southern Appalachians. For. Sci. **36**(4): 917–929.

Long, Z.T., Pendergast, T.H., IV, and Carson, W.P. 2007. The impact of deer on relationships between tree growth and mortality in an old-growth beech-maple forest. For. Ecol. Manage. **252**: 230–238. doi:10.1016/j.foreco.2007.06.034.

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

Lorimer, C.G. 1989. The oak regeneration problem: New evidence of causes and possible solutions. Forest Resource Analyses, No. 8. November 1989. Department of Forestry School of Natural Resources College of Agricultural and Life Sciences. University of Wisconsin-Madison. 31 p.

Lorimer, C.G., Chapman, J.W., and Lambert, W.D. 1994. Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. J. Ecol. **82**: 227–237. doi:10.2307/2261291.

McCarthy, B.C., Hammer, C.A., Kauffman, G.L., and Cantino, P.D. 1987. Vegetation patterns and structure of an old-growth forest in southeastern Ohio. Bull. Torrey Bot. Club, **114**: 33–45.

McGee, C.E. 1986. Loss of *Quercus* spp. dominance in an undisturbed old-growth forest. J. Elisha Mitchell Sci. Soc. **102**: 10–15.

McQuilkin, R.A. 1975. Growth of four types of white oak reproduction after clearcutting in the Missouri Ozarks. USDA Forest Service Research Paper NC-116.

Merz, R.W., and Boyce, S.G. 1956. Age of oak "seedlings". J. For. **54**(11): 664–775.

Nowacki, G.J., and Abrams, M.D. 1992. Community, edaphic, and historical analysis of mixed oak forests of the Ridge and Valley Province in central Pennsylvania. Can. J. For. Res. **22**(6): 790–800. doi:10.1139/x92-108.

Nowacki, G.J., and Abrams, M.D. 2008. The demise of fire and "mesophication" of forests in the eastern United States. BioScience, **58**(2):123–138. doi:10.1641/B580207.

Nowacki, G.J., Abrams, M.D., and Lorimer, C.G. 1990. Composition, structure, and historical development of northern red oak stands along an edaphic gradient in north-central Wisconsin. For. Sci. **36**: 276–292.

Nuttle, T., Royo, A.A., Adams, M.B., and Carson, W.P. 2013. Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. Ecol. Monogr. **83**(1): 3–17. doi:10.1890/11-2263.1.

Pan, C., Tajchman, S.J., and Kochenderfer, J.N. 1997. Dendroclimatological analysis of major forest species of the central Appalachians. For. Ecol. Manage. **98**: 77–87. doi:10.1016/S0378-1127(97)00087-X.

Peterson, D.W., and Reich, P.B. 2001. Prescribed fire in oak savanna: Fire frequency effects on stand structure and dynamics. Ecol. Appl. **11**(3): 914–927. doi:10.1890/1051-0761(2001)011[0914:PFIOSF]2.0.CO;2.

Porter, W.F., Mathews, N.E., Underwood, H.B., Sage, R.W., Jr., and Behrend, D.F. 1991. Social organization in deer: Implications for localized management. Environ. Manage. **15**(6): 809–814. doi:10.1007/BF02394818.

Quality Deer Management Association (QDMA). 2010. Whitetail map. Available from http://www.i-maps.com/Qdma/frame/default1024_ie.asp?C=48449&LinkID=0&NID=0&cmd=map&TL=100000&GL=010100&MF=11000 (Last accessed 26 April 2011).

Rentch, J.S., Fajvan, M.A., and Hicks, R.R. 2003. Oak establishment and canopy accession strategies in five old-growth stands in the central hardwood forest region. For. Ecol. Manage. **184**: 285–297. doi:10.1016/S0378-1127(03)00155-5.

Rooney, T.P. 2001. Deer impacts on forest ecosystems: a North American perspective. Forestry, **4**(3): 201–208. doi:10.1093/forestry/74.3.201.

Royo, A.A., Collins, R., Adams, M.B., Kirschbaum, C., and Carson, W.P. 2010. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. Ecology, **91**(1): 93–105. doi:10.1890/08-1680.1.

Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology, **62**(4): 1041–1051. doi:10.2307/1937003.

Sander, I.L. 1971. Height growth of new oak sprouts depends on size of advance reproduction. J. For. **69**(11): 809–811.

Sander, I.L. 1972. Size of oak advance reproduction: Key to growth following harvest cutting. USDA Forest Service Research Paper NC-79.

Sander, I.L., and Clark, F.B. 1971. Reproduction of upland hardwood forests in the central states. USDA Forest Service, Agriculture Handbook 405.

Sander, I.L., McGee, C.E., Day, K.G., and Willard, R.E. 1983. Oak-Hickory. *In* Silvicultural Systems for the Major Forest Types of the United States. *Edited by* R.M. Burns. Agric. Handbook 445, pp. 116–120.

SAS. 2006. SAS Enterprise Guide 4.1. SAS Institute Inc., Cary, NC, USA.

Schuler, T.M., Thomas-Van Gundy, M.A., Adams, M.B., and Ford, W.M. 2010. Seed bank response to prescribed fire in the Central Appalachians. USDA Forest Service Research Paper NRS-9.

Schuler, T.M., Thomas-Van Gundy, M.A., Adams, M.B., and Ford, W.M. 2013. Analysis of two pre-shelterwood prescribed fires in a mesic mixed-oak forest in West Virginia. *In* Proceedings of the 18th Central Hardwood Forest Conference; 2012 March 26–28; Morgantown, WV. *Edited by* Gary W. Miller, Thomas M. Schuler, Kurt W. Gottschalk, John R. Brooks, Shawn T. Gruschecky, Ben D. Spong, James S. Rentch. Gen. Tech. Rep. NRS-P-117. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station, pp. 430–446.

Signell, S.A., Abrams, M.D., and Hovis, J.C. 2005. Impacts of multiple fires on stand structure and tree regeneration in central Appalachian oak forests. For. Ecol. Manage. **218**: 146–158. doi:10.1016/j.foreco.2005.07.006.

Stephenson, S.L. 1993. Upland Forests of West Virginia. McClain Printing Co., Parsons, WV.

Tryon, E.H., and Powell, D.S. 1984. Root ages of advance hardwood reproduction. For. Ecol. Manage. **8**: 293–298. doi:10.1016/0378-1127(84)90061-6.

Waldrop, T.A., and Lloyd, F.T. 1991. Forty years of prescribed burning on the Santee fire plots: effects on overstory and midstory vegetation. *In* Fire and the Environment: Ecological and Cultural Perspectives: Proceedings of an international symposium. *Edited by* S.C. Nodvin and T.A. Waldrop. Gen. Tech. Rep. SE-69, USDA Forest Service, pp. 45–50.

Watts, W.A. 1979. Late Quaternary vegetation of central Appalachia and the New Jersey coastal plain. Ecol. Monogr. **49**(4): 427–469. doi:10.2307/1942471.

Wendel, G.W., and Smith, H.C. 1986. Effects of a prescribed fire in a central Appalachian oak-hickory stand. USDA Forest Service Research Paper NE-594.

Wood, K.U.M. 2010. Ecological and economic impacts of wildfires on an Appalachian oak forest in southern West Virginal. M.Sc. thesis, West Virginia University, Morgantown, WV.

Woods, F.W., and Shanks, R.E. 1959. Natural replacement of chestnut by other species in the Great Smoky Mountains National Park. Ecology, **40**(3): 349–361. doi:10.2307/1929751.