THE FIRE AND OAK HYPOTHESIS: INCORPORATING THE INFLUENCE OF DEER BROWSING AND CANOPY GAPS

Rachel J. Collins and Walter P. Carson[1]

ABSTRACT.—A century of fire suppression has altered tree species composition and is a commonly cited cause for the region-wide decline in oak abundance (the fire and oak hypothesis). Other explanations include alterations in canopy gap regimes and deer browsing that operate in conjunction with fire suppression. We examined the interactions among these processes by manipulating fire, deer browsing, and canopy gaps, in a fully factorial design. Fire lowered survival of small canopy trees (10-19.9 cm DBH) but had no effect on large canopy trees ($\geq$20 cm DBH). Fire increased and deer browsing decreased the proportion of top-killed saplings that sprouted. Gaps, however, had no significant effect on sprouting. Deer browsing, after fire, reduced diversity in the sprouting community, created understories dominated by striped maple. Northern red oak saplings were not fire tolerant and did not produce tall sprouts following fire. These results cast doubt on the ubiquitous application of the fire and oak hypothesis to explain the dominance of oak in some mixed hardwood forests.

Historically, re-occurring fire may have caused oak to be common across much of the eastern deciduous forest: The fire and oak hypothesis (Abrams 1992). Proponents of the fire and oak hypothesis argue that a century of fire suppression is tied not only to a decline in the abundance of oak but a concomitant increase in the abundance of maple and other mesic species (Crow 1988, Brose and others 2001). Fire could promote oak if oaks survived fire in greater proportions than co-occurring species (Lorimer 1985). Oaks may increase in relative abundance following fire either via lower stem mortality or a greater capacity for sprouting or both (Crow 1988, Abrams 1992, Van Lear and Watt 1992). Both the ability of trees to survive fire and sprout following fire varies widely among species (Wright and Bailey 1982). Re-occurring fire may have favored sprouting as a major pathway of regeneration because it skips the vulnerable early establishment phase (Bond and Midgley 2001). Overall, fire can structure forest communities and set successional trajectories through species' differential tolerances to fire.

The abundance of oak is typically correlated with fire frequency. For example, frequent, re-occurring fires over the past 10,000 years are associated with periods of high oak abundance (Delcourt and Delcourt 1987). Guyette and Dey (1996) and Abrams (1992) argued that logging, circa 1900, and subsequent fires expanded the dominance of oak into areas (e.g., Ontario and Wisconsin) that were formerly dominated by more mesic species such as beech and maple. In the last 50 years, more mesic and putatively fire intolerant species have invaded the understory of mature oak forests, where fires have been largely suppressed for a hundred years (Lorimer 1984). Although these studies provide strong support for a role of fire in oak forest dynamics, the evidence remains circumstantial and correlative.

Some prescribed fire studies have supported the fire and oak hypothesis particularly when applied to northern red oak. Canopy oaks typically have high survival following prescribed fire of low to intermediate intensity (Elliott and others 1999) and often survive in higher proportions relative to some

---

[1] Doctoral Candidate (RJC) and Associate Professor (WPC), Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260. RJC and WPC are corresponding authors: to contact, call (717) 254-8918 or e-mail at collinsra@dickinson.edu or call (412) 624-5496 or email at walt+@pitt.edu.

Citation for proceedings: Van Sambeek, J.W.; Dawson, J.O.; Ponder, F., Jr.; Loewenstein, E.F.; Fralish, J.S., eds. 2003. Proceedings, 13th Central Hardwood Forest conference; 2002 April 1-3; Urbana, IL. Gen. Tech. Rep. NC-234. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Research Station. 565 p. [Peer-reviewed paper from oral presentation].

co-occurring species (Brose and Van Lear 1999). Understory oaks vary in their response to prescribed fires. In some cases, oak seedlings and saplings sprout in higher proportions, have greater survival, and have greater growth rates following fire compared to co-occurring species (Christensen 1971, Huddle and Pallardy 1996, Brose and Van Lear 1998). For example, in Wisconsin, small prescribed fires increased the relative densities of oak seedlings in forest openings (Kruger and Reich 1997). In contrast, other researchers have found that the abundance of northern red oak seedlings decreased after fires (Wendel and Smith 1986, Merritt and Pope 1991, Elliott and others 1999).

Because site-specific factors likely interact with the effects of surface fire on tree species survival, it is not surprising that little consensus about the effects of fire on oak has emerged from a handful of prescribed fire experiments. For example, deer browsing and canopy gaps strongly favor some species over others and the degree to which these factors operate varies greatly across forest types and landscapes (Ehrenfeld 1980, Marquis 1981, Runkle 1990, Castleberry and others 2000). How these two factors interact with fire remains little more than speculation but may be central to an understanding of forest dynamics in the eastern USA.

Deer herbivory can dramatically alter species composition in the seedling and sapling layer due to both interspecific differences in palatability and differential survival and regrowth following browsing (Anderson and Loucks 1979, Tilghman 1989, Ford and others 1994, Kittredge and others 1995). Further, deer may preferentially browse in burned areas due to an increase in forage (Masters and others 1993). For example, Gordon and others (1995) found that oak seedling growth was lower in burned sites and attributed this to intense browsing by deer. Studying fire without explicitly considering the impact of browsing could lead to spurious conclusions.

Similar to deer browsing, canopy gaps can alter species composition in the understory due to interspecific differences in shade tolerance among seedlings and saplings (Ehrenfeld 1980). In canopy gaps, species that are intermediate in shade tolerance, such as northern red oak, may be able to regenerate (Kline and Cottam 1979, Barden 1981). In fact, Nyland and others (1982) found that oak saplings were present almost entirely in canopy gaps. Furthermore, Runkle (1990) demonstrated that canopy gaps permit some species to regenerate in the absence of stand replacement disturbance and thus can maintain tree species diversity in forests. Additionally, deer may preferentially browse on abundant sprouts found in forest openings compared to closed canopy areas (Butterworth and Tzilkowski 1990, Castleberry and others 2000). Because interactions are important and understudied, we argue that it is time to move beyond hypotheses that narrowly focus on a single factor (e.g., the Fire and Oak Hypothesis) when the influence of other factors are well demonstrated.

Overall, there is ample evidence to argue that fire, canopy gaps, and browsing will all interact to strongly influence the diversity and relative abundance of understory trees. Here, we experimentally evaluated the influence of canopy gaps, deer browsing, and fire on canopy survival and sapling sprouting of 14 common tree species using a factorial design (see Appendix table 1 for plant species code, scientific, and common names). In particular, we tested the predictions of the fire and oak hypothesis that

1) a greater proportion of northern red oak canopy trees will survive fire than co-occurring species, and
2) after prescribed fires, a greater proportion of top-killed northern red oak saplings will resprout than co-occurring species.

We go on to expand the fire hypothesis by explicitly considering the potential interactions of deer browsing and canopy gaps on a community of co-occurring species.

METHODS

Study Area and Design

We conducted this study in four 20 to 40 ha stands at the Westvaco Research Forest (WRF) in Randolph County, in north-central West Virginia. The WRF encompasses 3,500 ha and lies within the mixed mesophytic forest region (Cumberland and Allegheny Plateaus) of the eastern deciduous forest (Braun 1967). The four stands had slopes from 10 to 31 percent, were between 800 to 1,000 m in elevation, and ranged in age from 64 to 77 years. Basal area for these stands was between 22 and 28 m^2/ha with site indexes ranging from 21-24 m (70-80 ft for northern red oak at 50 years). We chose stands that had not been logged or thinned in more than 15 years, that had a closed canopy, and were devoid of signs of recent major disturbance including large canopy gaps and fire. Although sugar maple dominated both the canopy and sapling layers, the stands were relatively diverse and typical of mixed mesophytic/ northern hardwood transition forests (table 1).

The study was installed as a split-plot design. Within each of the four stands, we established 16, 400 m^2 plots (20 by 20 m) in 1997. All plots were located at least 20 m from other plots, stand edges, and fire breaks. We avoided canopy gaps and large rock outcroppings. Half of each stand, including 8 of the 16 plots, was randomly assigned to a burned treatment or an unburned control treatment. Within each half, each of the following four treatments, fence (no deer browsing), canopy gap (250 m^2), fence x canopy gap, and neither a fence nor gap, were randomly applied to two of the eight plots.

Treatments

We created 32 canopy gaps (~18 m in diameter, 250 m^2) by girdling and injecting herbicide (Accord® by Monsanto) into trees (DBH > 10 cm) located in the center of each plot in the spring of 1998 and erected deer proof fences around 32 plots immediately thereafter. We excluded deer with 2 m tall fences constructed from 14 gauge farm and field woven wire fencing reinforced with iron rods (rebar) and metal posts erected in the summer of 1998. These fences primarily excluded white-tail deer (*Odocoileus virginianus*). The mesh size was approximately 30 x 15 cm allowing small to medium sized animals (e.g., raccoons) to pass through and other animals could fly or climb over (e.g., turkey and black bear). We found no deer hoof prints during snow cover or deer scat in any season inside fences. We refer to the fence treatment as “no-deer” for the remainder of the paper.

Four 10 to 20 ha fires were conducted between 30 April and 4 May 1999 after 6 to 10 days of no rain. The fires occurred during the sapling layer bud break, which we observed occurs 1 to 2 weeks prior to canopy layer bud break. Fuel loads ranged from 237 to 325 kg/ha of leaf litter and small woody debris (≤ 3 cm diameter, dry weight directly sampled in 192, 0.25 m^2 quadrates) and 1,450 to 2,540 kg/ha of course woody debris (estimated). Air temperature ranged from 20° to 23° C, relative humidity ranged from 20 to 28 percent, winds ranged from 0 to 13 kph. Fires were started from late morning to mid afternoon using strip head fires. Strips were set from 20 to 60 m apart using drip torches. Fires were hot and mean temperatures per fire ranged from 215° to 440° C at the ground level measured with 128 temperature sensors made from Tempilax® temperature sensitive liquid following the procedure described by Cole and others (1992). Percent of ground burned per fire ranged from 78 to 100 percent.

Plot Census Data

In 1997, the year prior to commencing treatments, we identified, permanently tagged, mapped, and

Table 1.—*Species composition in the canopy layer (≥10 cm DBH) and sapling layer (10-9.9 cm DBH). Density (stems/ha), SE and percent of stand are means of the four stands*

Species	Density	SE	Percent
CANOPY LAYER			
Sugar maple	223.05	55.70	42.6
American beech	66.02	40.59	12.6
Red maple	52.73	17.52	10.1
Basswood	42.58	15.41	8.1
Magnolia	27.34	19.12	5.2
Birch	20.70	7.93	4.0
Northern red oak	20.31	7.99	3.9
Black cherry	19.14	5.93	3.7
Yellow poplar	15.23	6.33	2.9
White ash	14.45	2.81	2.8
Hickory	6.25	3.55	1.2
Chestnut oak	4.30	4.30	0.8
Sourwood	3.91	3.41	0.7
Black locust	3.13	0.64	0.6
Eastern hemlock	2.73	2.24	0.5
Ironwood	1.56	0.64	0.3
Striped maple	0		0.0
Witch hazel	0		0.0
Total	525.39	27.03	
SAPLING LAYER			
Sugar maple	1,442.97	67.06	47.3
American beech	544.92	325.53	17.9
Red maple	90.63	66.53	3.0
Basswood	18.36	5.79	0.6
Magnolia	53.52	29.05	1.8
Birch	81.64	28.32	2.7
Northern red oak	14.84	8.80	0.5
Black cherry	218.36	81.18	7.2
Yellow poplar	10.55	3.15	0.3
White ash	16.02	9.79	0.5
Hickory	11.33	7.14	0.4
Chestnut oak	0		0.0
Sourwood	0		0.0
Black locust	0		0.0
Eastern hemlock	0		0.0
Ironwood	38.67	5.68	1.3
Striped maple	458.98	226.55	15.1
Witch hazel	48.83	33.01	1.6
Total	2,941.06	548.69	

recorded DBH for all trees greater than 140 cm tall for a total of 636 canopy trees (> 10 cm DBH) and 7,905 saplings (1-10 cm DBH). We remeasured all trees in all plots in June and July 1999 and 2000. Trees were designated as alive or dead. Saplings were designated as alive, top-killed with sprouts, or top-killed without sprouts. We also quantified the number of sprouts on all top-killed saplings and measured the height of the tallest sprout. We used "top-killed" to describe saplings where the original aboveground biomass was dead when we remeasured. We used "top-killed with sprouts" to describe top-killed saplings that had new shoots originating from near the root collar during the recensuses.

Canopy Tree Survival

We analyzed survival among treatments in two size classes of canopy trees (small: 10-19.9 cm; and large: ≥ 20 cm DBH) on a per plot basis for the 10 most common species (table 1). Because we girdled canopy trees in gap plots, we excluded gap treatments from all survival analyses; this included plots where gaps were crossed with other treatments (i.e., NO-DEER X GAP, FIRE X GAP, FIRE X NO-DEER X GAP). Because percent survival for many species and plots was close to 100 percent, we performed an arcsine transformation on all of the proportional survival data to normalize the distributions (Sokal and Rohlf 1995). We tested mean survival for all species combined with an ANOVA using a split-plot, two-way factorial design with FIRE as the main factor and NO-DEER, canopy tree SIZE, and NO-DEER X SIZE as within plot factors. For this and all following analyses that included FIRE as a factor, the F-statistics for the main-plot effect of FIRE was calculated using the STAND X FIRE interaction term as the denominator (Littell and others 1993). Furthermore, the F-statistic for all within plot factors were calculated using the residual mean squared error as the denominator.

In a separate analysis, red maple, sugar maple, American beech, and basswood each occurred in enough plots to test if there was differential survival among species. Species had to occur in at least four plots in both size classes to be included in the analysis. For these species level analyses, we conducted a split-plot ANOVA as above, except with SPECIES (instead of NO-DEER) as a within plot factor. We used least squared means and orthogonal contrasts to examine significant interactions.

Sapling Sprouting Response

We calculated the percentage of top-killed saplings (1-10 cm DBH) that sprouted for the 14 most common species per plot. Because percent sprouting for many species and plots was close to 0 percent, we performed an arcsine transformation on all of the proportional sprouting data to normalize the distributions (Sokal and Rohlf 1995). We classified top-killed saplings with sprouts into two overlapping categories:

(1) all individuals with sprouts greater than 1 cm tall and
(2) all individuals with sprouts greater than 50 cm tall.

We divided sprouts into these two categories because this identified vigorous sprouts from the ones that sprouted and failed to grow. We used an ANOVA with a split-plot, two-way factorial design to test for the effects of the treatments (FIRE, NO-DEER, GAPS) and their interactions on mean sprouting response for all species combined that had sprouts that were greater than 1 cm tall. FIRE was the main factor and NO-DEER, GAP and NO-DEER X GAP were the within plot factors.

We conducted three analyses on saplings with tall sprouts (> 50 cm tall). First, we used an ANOVA with a split-plot, two-way factorial design to test for the effects of the treatments (FIRE, NO-DEER, GAP) and their interactions on mean sprouting response for all species combined. FIRE was the main factor and NO-DEER, GAP, and NO-DEER X GAP were the within plot factors. Second, we tested for the effects of FIRE, GAP, and SPECIES on sprouting response in the absence of herbivory (i.e., all of the NO-DEER plots: NO-DEER, NO-DEER X GAP, FIRE X NO-DEER, and FIRE X NO-DEER X GAPS). We used an ANOVA with the same split-plot, two-way factorial design as the previous analysis except with SPECIES, instead of NO-DEER, as a within plot factor. Here a significant interaction of SPECIES X FIRE or SPECIES X GAP demonstrates species-specific sprouting responses to fire or gaps in the absence of any browsing pressure. The species we included in this analysis were striped maple, red maple, sugar maple, American beech and black cherry because each occurred in at least three plots.

Lastly, we further examined the effects of gaps and species on sprouting response on 14 species in the absence of herbivory and following fire (i.e., FIRE X NO-DEER plots versus FIRE X NO-DEER X GAP PLOTS). We used a two-way factorial ANOVA with SPECIES, GAP, and their interaction as factors. If the GAP X SPECIES interaction was not significant, we combined these two treatments and compared sprouting response of 14 species in the community. The species included were: striped maple, red maple, sugar maple, birch, hickory, American beech, white ash, witch hazel, yellow poplar, magnolia, ironwood, black cherry, northern red oak, and basswood. We used least squared means and orthogonal contrasts to explore significant interactions.

RESULTS

Canopy Tree Survival

As expected, deer browsing did not significantly influence the survival of canopy trees (P > 0.2; table 2). Therefore, for all remaining canopy survival analyses, we pooled control plots and no-deer plots (the no fire treatment) and pooled fire plots and fire x no-deer plots (the fire treatment). For all species combined, fire killed a significant proportion of small canopy trees

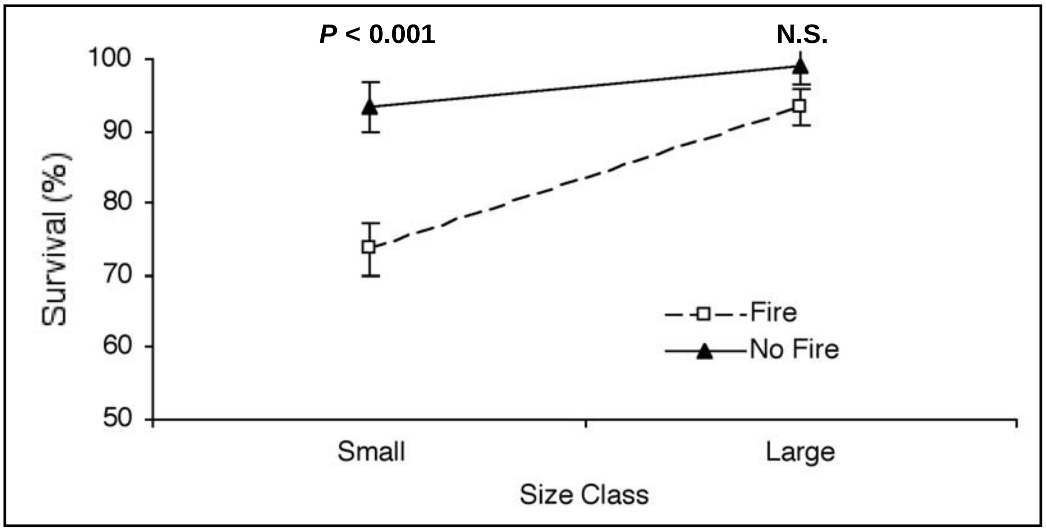

Figure 1.—*Mean canopy tree survival (± 1 SE) of trees in fire and no-fire treatments and in two size classes: large (> 20 cm DBH) and small (10-19.9 DBH).*

Table 2.—*Mean canopy tree survival (± 1 SE) per 400 m² plot for 10 common species and two size classes*

	Fire treatments[1]						**No-fire treatments**[2]					
	Small 10-19.9 cm DBH			**Large ≥20 cm DBH**			**Small 10-19.9 cm DBH**			**Large ≥20 cm DBH**		
	Mean	**SE**	**N**[3]	**Mean**	**SE**	**N**[3]	**Mean**	**SE**	**N**	**Mean**	**SE**	**N**[3]
ACRU[4]	50.00	22.36	6	80.95	14.29	7	100.00	0.00	8	100.00	0.00	10
ACSA	75.48	7.51	15	100.00	0.00	14	95.40	2.71	14	100.00	0.00	13
BESP	100.00		1	100.00	0.00	4	100.00	0.00	2	94.44	5.56	9
FAGR	78.57	16.39	6	85.71	14.29	7	100.00	0.00	6	96.30	3.70	9
FRAM	50.00		1	100.00	0.00	3			0	100.00	0.00	6
LITU	100.00		1	92.86	7.14	7	100.00		1	100.00	0.00	5
MASP	100.00		1	70.00	20.00	5	80.00	20.00	5	100.00	0.00	4
PRSE			0	95.83	4.17	8			0	100.00	0.00	6
QURU			0	100.00	0.00	7			0	100.00	0.00	11
TIAM	80.00	20.00	5	100.00	0.00	9	75.00	25.00	4	100.00	0.00	6

[1] Fire treatments included fire and fire x no-deer plots (Maximum N = 16).
[2] No-fire treatments included control and no-deer plots (Maximum N = 16).
[3] N varies because not all species and size classes occurred in all plots.
[4] Species names are described Appendix table 1.

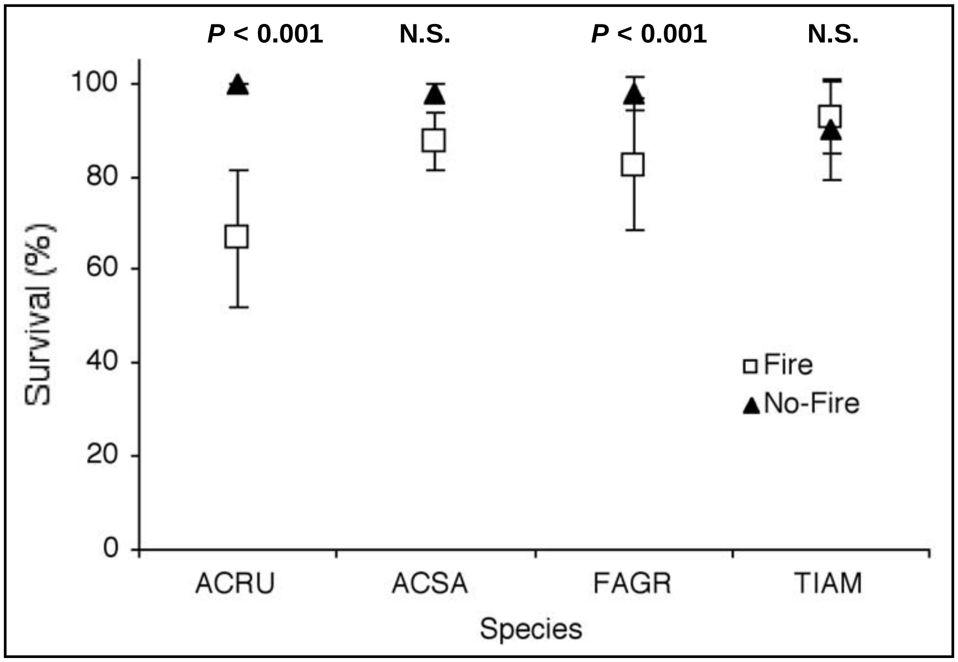

Figure 2.—*Mean canopy tree survival (± 1 SE) of trees in fire and no-fire treatment for red maple, sugar maple, American beech, and basswood.*

(10-19.9 cm DBH) but had no significant effect on large canopy trees (> 20 cm DBH; $p < 0.05$, table 2, fig. 1). We found no significant effect of fire on large canopy trees.

There were no species-specific effects of size regardless of fire (FIRE X SIZE X SPECIES interaction not significant). Fire killed a greater proportion of primarily small red maple and American beech (fig. 2), and had no significant effect on sugar maple and basswood (FIRE X SPECIES interaction, $p < 0.05$, Appendix table 3). Note that there were no individuals of oak in the small canopy size classes (table 2).

Sprouting Behavior

General Sprouting Responses

Of the nearly 8,000 individual saplings we monitored, 4,155 were classified as top-killed or top-killed with sprouts during the second growing season following fire. A greater proportion of top-killed saplings produced sprouts (>1 cm tall) in fire plots and in no-deer plots than saplings without fire or browsed by deer (fig. 3A). Additionally, top-killed saplings of most species produced sprouts (table 3). Gaps, however, did not significantly affect the proportion of top-killed saplings that sprouted ($P > 0.6$; table 4). We restricted the remaining analyses to top-killed saplings that produced tall, vigorous sprouts greater than 50 cm tall.

Tall Sprouts In Fire And No Fire Areas

Deer browsing decreased the number of top-killed saplings that produced tall sprouts (fig. 3B). This response was greatly magnified in the fire treatment (fig. 4). Following fire, deer browsing reduced diversity of large sprouts from 12 to 2 species (table 4). Only striped maple and red maple had large sprouts outside of fences in fire plots. Gaps did not have a significant effect on sprouting behavior ($P > 0.1$; table 5).

Tall Sprouts In The No-Deer Plots Including Fire And No Fire Areas

We tested for interspecific differences in sprouting behavior among the five most abundant species that had top-killed individuals in both the fire and no fire areas. We used only five species to compare fire and no fire areas because so few individuals were top-killed in the unburned areas. Additionally, we only conducted this analysis for no-deer plots because browsing by deer drastically reduced the number of species that produced sprouts over 50 cm (table 4). Our goal was to evaluate species-specific sprouting potential without the pervasive and damaging effect of browsing. Again, gap did not affect sprouting response ($P > 0.3$, Appendix table 6). Figure 5 shows that fire did have a species-specific effect on sapling sprouting (FIRE X SPECIES interaction, $P < 0.001$). Striped maple and black cherry sprouted in similar proportions in the burned and unburned plots ($P > 0.05$). Top-killed red maple

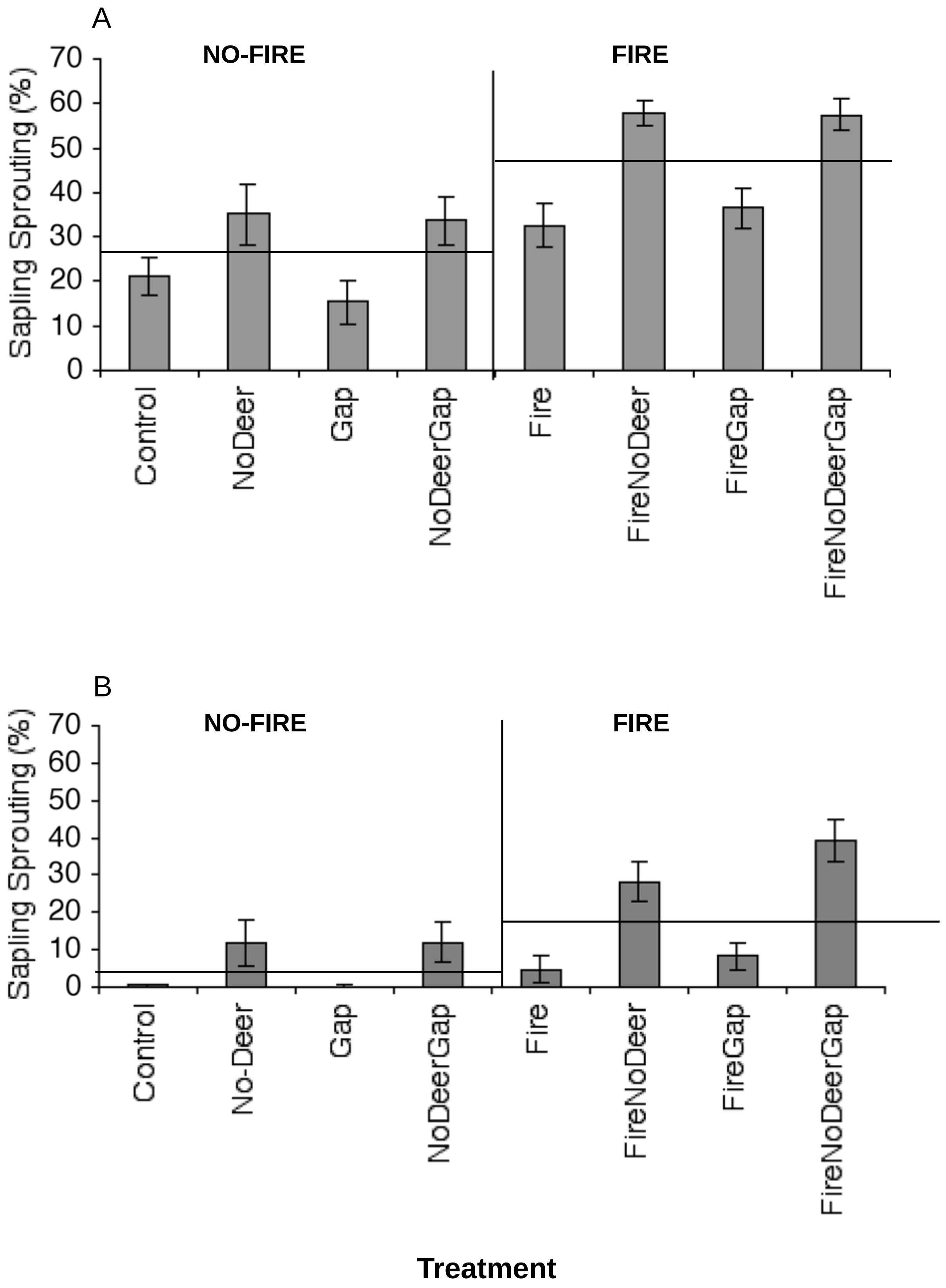

Figure 3.—*Mean percent sprouting of top-killed saplings for all species combined within each treatment (± 1 SE; N=8) for (A) all sprouts (> 1 cm tall) and for (B) tall sprouts (> 50 cm tall). All species are combined. Horizontal lines are fire and no-fire treatment means.*

Table 3.—*Mean percent (± 1 SE) of top-killed saplings that produced sprouts > 1 cm tall in eight treatments. Means > 5% in > 1 plot are in bold.*

	NO-FIRE TREATMENTS											
	Control			**No-Deer**			**Gap**			**No-deer x gap**		
Species[1]	**Mean**	**SE**	**N[2]**	**Mean**	**SE**	**N[2]**	**Mean**	**SE**	**N[2]**	**Mean**	**SE**	**N[2]**
ACPE	**36.02**	**11.75**	**6**	**29.72**	**15.09**	**6**	4.76	4.76	3	**55.00**	**20.00**	**5**
ACRU	0.00	0.00	4	25.00	25.00	2	**11.11**	**11.11**	**3**	100.00	.	1
ACSA	4.28	2.28	7	**31.93**	**10.70**	**7**	3.31	2.36	8	**29.29**	**13.65**	**7**
BESP	0.00	0.00	4	0.00	0.00	2	0.00	0.00	2	0.00	0.00	2
CASP	**75.00**	**25.00**	**2**	100.00	.	1				0.00	.	1
FAGR	**37.50**	**21.04**	**4**	**24.67**	**10.41**	**5**	**20.83**	**12.50**	**4**	**33.33**	**33.33**	**3**
FRAM	60.00	.	1				**8.33**	**8.33**	**3**	100.00	.	1
HAVI										0.00	.	1
LITU							100.00	.	1			
MASP	**16.67**	**16.67**	**3**	100.00	.	1	**16.67**	**16.67**	**2**	100.00	.	1
OSVI	0.00	0.00	3				0.00	0.00	2			
PRSE	**47.50**	**16.01**	**5**	**56.82**	**16.89**	**3**	**56.57**	**21.73**	**3**	**45.00**	**5.00**	**2**
QURU	33.33	.	1				**50.00**	**50.00**	**2**			
TIAM	50.00	.	1	0.00	0.00	2	0.00	.	1	0.00	.	1

	FIRE TREATMENTS											
	Fire			**Fire x no-deer**			**Fire x gap**			**Fire x no-deer x gap**		
Species	**Mean**	**SE**	**N[2]**	**Mean**	**SE**	**N[2]**	**Mean**	**SE**	**N[2]**	**Mean**	**SE**	**N[2]**
ACPE	**24.01**	**9.47**	**7**	**43.19**	**8.52**	**8**	**55.03**	**13.75**	**6**	**56.03**	**8.33**	**5**
ACRU	**55.56**	**29.40**	**3**	**91.67**	**8.33**	**4**	**44.74**	**22.37**	**3**	**63.05**	**12.71**	**5**
ACSA	**27.89**	**5.52**	**8**	**60.53**	**2.39**	**8**	**16.18**	**4.62**	**8**	**60.06**	**5.68**	**8**
BESP	0.00	0.00	3	**14.06**	**12.07**	**4**	0.00	0.00	5	0.00	0.00	5
CASP	66.67	.	1	**66.67**	**33.33**	**3**	0.00	.	1	100.00	.	1
FAGR	**72.22**	**8.81**	**5**	**53.92**	**12.76**	**5**	**56.64**	**14.06**	**6**	**53.63**	**13.92**	**7**
FRAM	0.00	0.00	2	0.00	.	1	**33.33**	**33.33**	**2**	0.00	.	1
HAVI	**42.75**	**9.42**	**2**	**59.62**	**9.62**	**2**	50.00	.	1	**66.67**	**9.62**	**3**
LITU	**25.00**	**25.00**	**2**	**68.75**	**23.66**	**4**	**50.00**	**50.00**	**2**	**50.00**	**.**	**1**
MASP	**33.33**	**33.33**	**3**	50.00	.	1	**16.67**	**16.67**	**3**	**66.67**	**33.33**	**3**
OSVI	**16.67**	**16.67**	**3**	**23.47**	**2.41**	**3**	**61.11**	**20.03**	**3**	**13.33**	**13.33**	**3**
PRSE	**36.15**	**11.11**	**5**	**76.07**	**8.30**	**5**	**48.84**	**17.80**	**5**	**64.04**	**19.11**	**4**
QURU	0.00	.	1	0.00	.	1	**50.00**	**50.00**	**2**	0.00	0.00	3
TIAM	0.00	.	1	**25.00**	**25.00**	**2**	**46.67**	**22.61**	**5**	**33.33**	**33.33**	**3**

[1] Maximum possible N is 8. N varies because not all species occurred in all plots.

[2] Species names are described in Appendix table 1.

and sugar maple sprouted copiously following fire, but did not sprout in unburned areas ($P < 0.01$).

Tall Sprouts In No-Deer Plots In Fire Plots Only

We examined the interspecific differences in sprouting behavior among the 14 most abundant species within burned sites. GAP and GAP X SPECIES interaction did not affect sprouting response ($P > 0.15$ and $P > 0.76$, respectively). Therefore, we combined data from FIRE X NO-DEER plots with FIRE X NO-DEER X GAP plots to evaluate species-specific sprouting responses (fig. 6). Hickory, yellow poplar, witch hazel, magnolia, red maple, and black cherry all sprouted in greater proportion than the mean for all individuals (31 percent) for all the common species in the community. Striped maple, basswood, and sugar maple had an intermediate response at or near the mean. Ironwood, birch, American beech, white ash, and northern red oak all sprouted at proportions well below the mean.

DISCUSSION

We examined the fire and oak hypothesis in mixed hardwood stands where oaks were present but uncommon. Others have suggested that mixed hardwood stands with a low occurrence of oak regeneration best characterize the classic failed oak regeneration pattern due to fire suppression (Abrams 1992, Lorimer 1992, Brose

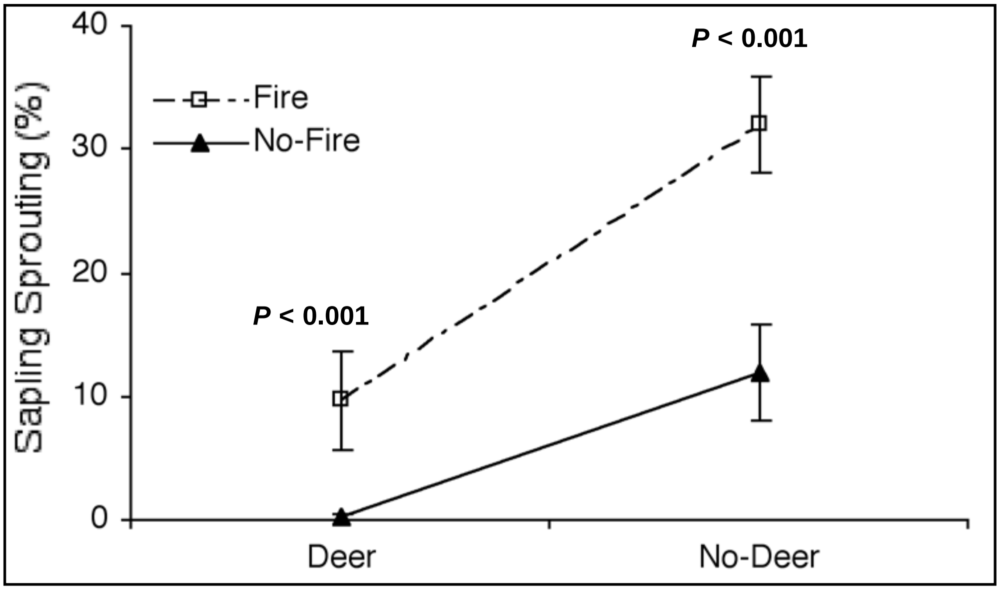

Figure 4.—*Mean percent sprouting (± SE) of top-killed saplings with sprouts > 50 cm tall in fire and no-fire treatments and deer and no-deer treatments.*

and others 2001). When prescribed fires have failed to increase the relative abundance of oak, others have suggested that fires were too low in intensity or a single fire is insufficient to promote oak abundance. Published evidence that multiple fires promote oak abundance is weak. Nyland and others (1982) had one site where they conducted two fires and presented no vegetation data or statistics. Merritt and Pope (1991) found that the effects of two fires on northern red oak seedlings were not different from the effects of one fire. Lastly, Huddle and Pallardy (1996) found that multiple fires decreased red oak abundance. The areas we burned in this study likely had historical fire return times on the century scale and did not experience frequent understory fires set by pre-Columbian humans as occurred in other regions (Abrams 1992, Guyette and Dey 2000, Brose and others 2001).

Fire could promote oak's dominance in forest communities in two ways: by promoting the relative density of oak while leaving other species unchanged or by decreasing the relative density of co-occurring species and leaving oaks unchanged or a combination of both of these. Lorimer (1992) suggested that the latter is more important but, to date, empirical evidence is equivocal. Determining which of these two processes is more prevalent is important to understanding how fire and its interactions with other processes structure communities. In this study, we examined the relative contribution of these two processes.

Testing Prediction 1: Canopy Tree Survival

The first prediction we tested was that northern red oak canopy trees will survive fire in a higher proportion than co-occurring species. Even though fire caused species-specific mortality in small canopy trees, we could not test this prediction because there were no small oak canopy trees. Large northern red oak canopy trees (> 20 cm DBH) had 100 percent survival following fire, but so did large sugar maple, white ash, basswood, and birch. The latter two species are considered extremely fire intolerant (Burns and Honkala 1990). Although we did not find support for the fire and oak hypothesis in canopy trees, our data do demonstrate that even "fire intolerant" species can reach size refuges.

Size refuges, above which fire can not extirpate canopy tree species from an area, have been documented for some species since at least the mid-1980s (White 1983, Harmon 1984). In a 3-decade long study, Huddle and Pallardy (1996) demonstrated that post oak (*Q. stellata*) reached a size refuge around 15 to 20 cm DBH, above which repeated fires did not affect survival. Hickory species could also reach a size refuge under some conditions. Conversely, red oak species, which included northern red oaks, never reached a size refuge. Survival was based on canopy pretreatment size and the authors did not report sizes greater than 20 cm DBH (Huddle and Pallardy 1996).

In two other elaborate and extensive prescribed fire experiments, however, researchers failed to take canopy tree size into account in analyses

Table 4.—*Mean percent (± 1 SE) of top-killed saplings that produced sprouts > 50 cm tall in eight treatments. Means > 5% in > 1 plot are in bold*

NO-FIRE TREATMENTS												
	Control			No-deer			Gap			No-deer x gap		
Species[1]	Mean	SE	N[2]	Mean	SE	N[2]	Mean	SE	N[2]	Mean	SE	N[2]
ACPE	0.00	0.00	6	**18.75**	**16.38**	**6**	1.59	1.59	3	**42.50**	**23.58**	**5**
ACRU	0.00	0.00	4	0.00	0.00	2	0.00	0.00	3	0.00	.	5
ACSA	0.00	0.00	7	2.86	2.86	7	0.00	0.00	8	2.86	2.86	8
BESP	0.00	0.00	4	0.00	0.00	2	0.00	0.00	2	0.00	0.00	5
CASP	0.00	0.00	2	0.00	.	1	.	.	0	0.00	.	1
FAGR	0.00	0.00	4	0.00	0.00	5	0.00	0.00	4	**33.33**	**33.33**	**7**
FRAM	0.00	.	1	.	.	0	0.00	0.00	3	0.00	.	1
HAVI	.	.	0	.	.	0	.	.	0	0.00	.	3
LITU	.	.	0	.	.	0	0.00	.	1	.	.	1
MASP	0.00	0.00	3	100.00	.	1	0.00	0.00	2	**100.00**	**.**	**3**
OSVI	0.00	0.00	3	.	.	0	0.00	0.00	2	.	.	3
PRSE	1.00	1.00	5	**23.78**	**16.53**	**3**	0.00	0.00	3	**45.00**	**5.00**	**4**
QURU	0.00	.	1	.	.	0	0.00	0.00	2	.	.	3
TIAM	0.00	.	1	0.00	0.00	2	0.00	.	1	0.00	.	3
FIRE TREATMENTS												
	Fire			Fire x no-deer			Fire x gap			Fire x no-deer x gap		
Species	Mean	SE	N[2]	Mean	SE	N[2]	Mean	SE	N[2]	Mean	SE	N[2]
ACPE	**12.23**	**7.12**	**7**	**27.99**	**9.41**	**8**	**27.57**	**10.98**	**6**	**43.53**	**9.29**	**5**
ACRU	**11.11**	**11.1**	**3**	**58.33**	**25.00**	**4**	0.00	0.00	3	**54.38**	**13.57**	**5**
ACSA	0.09	0.09	8	**21.19**	**2.80**	**8**	0.45	0.45	8	**37.22**	**6.60**	**8**
BESP	0.00	0.00	3	**12.50**	**12.50**	**4**	0.00	0.00	5	0.00	0.00	5
CASP	0.00	.	1	**55.56**	**29.40**	**3**	0.00	.	1	100.00	.	1
FAGR	0.00	0.00	5	0.00	0.00	5	0.62	0.62	6	**7.14**	**7.14**	**7**
FRAM	0.00	0.00	2	0.00	.	1	0.00	0.00	2	0.00	.	1
HAVI	0.00	0.00	2	**59.62**	**9.62**	**2**	0.00	.	1	**66.67**	**9.62**	**3**
LITU	0.00	0.00	2	**68.75**	**23.66**	**4**	0.00	0.00	2	50.00	.	1
MASP	0.00	0.00	3	50.00	.	1	0.00	0.00	3	**66.67**	**33.33**	**3**
OSVI	0.00	0.00	3	**12.92**	**6.47**	**3**	0.00	0.00	3	**13.33**	**13.33**	**3**
PRSE	0.00	0.00	5	**51.10**	**14.23**	**5**	0.53	0.53	5	**44.41**	**21.42**	**4**
QURU	0.00	.	1	0.00	.	1	0.00	0.00	2	0.00	0.00	3
TIAM	0.00	.	1	**25.00**	**25.00**	**2**	0.00	0.00	5	**33.33**	**33.33**	**3**

[1] Species are described in Appendix table 1.

[2] Maximum possible N is 8. N varies because not all species occurred in all plots.

(Elliot and others 1999, Brose and Van Lear 1999). Elliot and others (1999) suggested that:

1) red maple (> 5 cm DBH) density decreased at high, fire intensity,
2) did not change at low fire intensity, and
3) that northern red oak (> 5 cm DBH) densities did not change across fire intensities.

In that study, it is possible that maples on average were smaller than the oaks. Similarly, Brose and Van Lear (1999) reported that oaks had about an 80 percent survival following fire compared to American beech and red maples that combined had about 50 percent survival after spring burns. However, they could not disentangle the effects of size from the effects of species because the oaks were overstory trees and the American beech and red maples were midstory trees (Brose and Van Lear 1999). Here, we reported survival of canopy trees in the second growing season following fire. Fire may have differentially damaged some trees that may die in the future causing the long term survival to differ from these short term results. However, we compared our results with other studies that reported survival of canopy trees 2 to 3 years following fire (Brose and Van Lear 1999, Elliot and others 1999.

The increase in abundance of red maple is considered a broad, region-wide, management

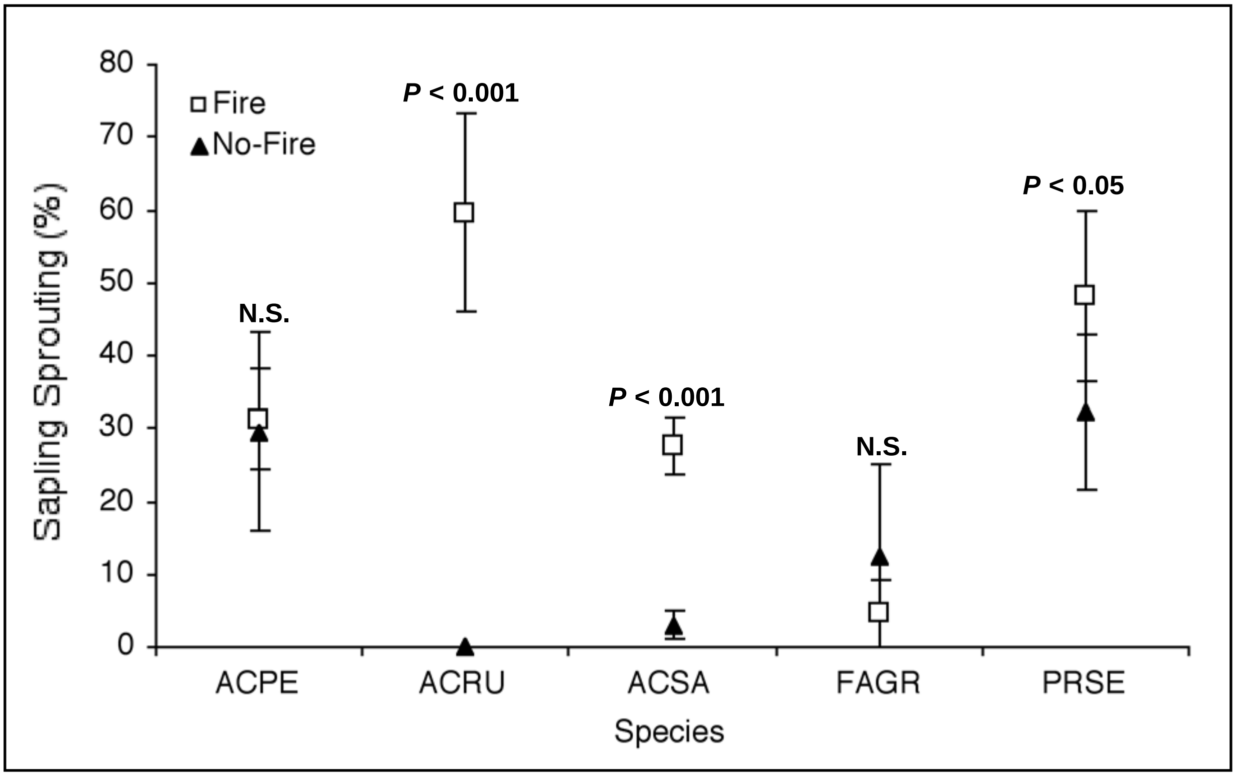

Figure 5—*Mean percent sprouting (± SE) of top-killed saplings with sprouts > 50 cm tall in fire and no-fire treatments for five common species: striped maple, red maple, sugar maple, American beech, and basswood.*

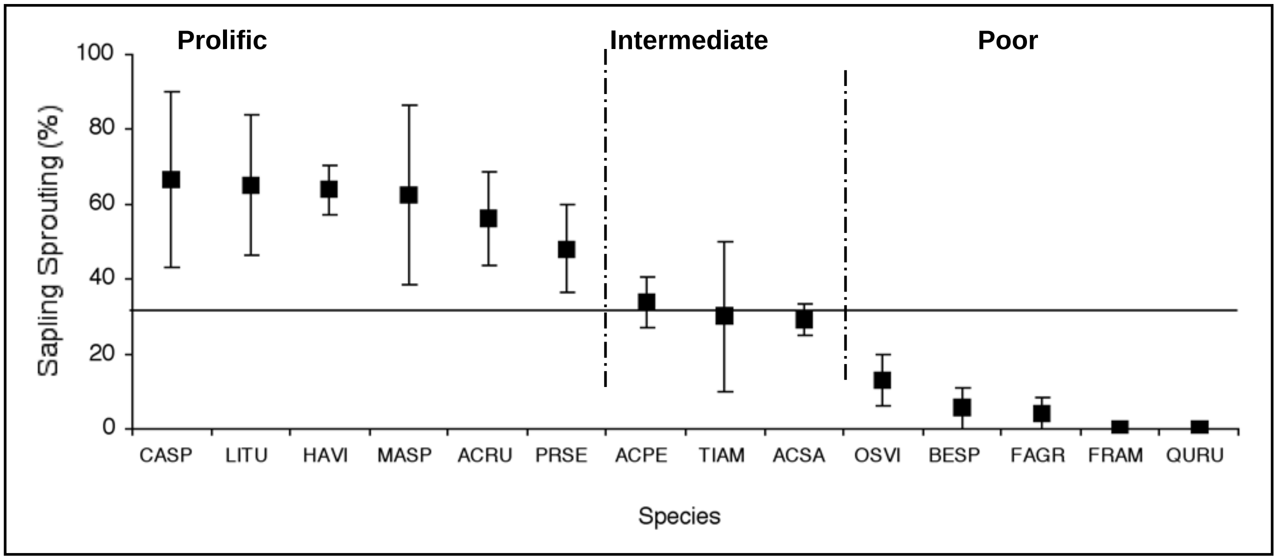

Figure 6.—*Mean sprouting of top-killed saplings (sprouts > 50 cm tall) ranked in descending order for 14 species in fire treatments (fire x no-deer plots and fire x no-deer x gap plots). The horizontal lines are the mean sprouting responses for the community. Species names are listed in Appendix table 1.*

problem (Abrams 1998). Advocates of the fire and oak hypothesis champion fire as a management tool that could reduce red maple while increasing northern red oak abundance (Van Lear and Watt 1992, Brose and others 2001). Our results suggest that fire can kill a significant proportion of small canopy red maples while leaving large northern red oak unaffected. However, no studies to date have adequately demonstrated comparative size-specific survival for both species. Such information is critical for managers. Additionally, Huddle and Pallardy (1996) recommend that managers should consider species composition, stand age, and other environmental stressors before applying prescribed fire, we concur.

Testing Prediction 2. Sapling Sprouting

The second predictions we tested was that top-killed northern red oak saplings would sprout in higher proportions than co-occurring species following fire. Oak saplings did not produce tall, vigorous sprouts that were likely to persist during this study. Many authors have argued that sprouting is the mechanism by which oak seedlings and saplings are fire tolerant (Crow 1988, Abrams 1992, Van Lear and Watt 1992, Johnson 1993, Brose and Van Lear 1998, Huddle and Pallardy 1999). However, evidence from the literature is ambiguous. Kruger and Reich (1997) conducted small burns (~200 m^2) in 0.5 ha openings that were fenced to remove deer browsing. Because nearly all seedlings were top-killed, the post-burn densities represented mainly seedling sprouting (~20 to 50 cm tall pre-treatment size). They found that northern red oak increased in relative density by nearly 50 percent whereas sugar maple density decreased by nearly 90 percent. Black cherry densities were unchanged.

In another study, Huddle and Pallardy (1999) planted nursery stock in a field that was then burned. Northern red oak survival was nearly four times greater than red maple survival. They attributed most of the oak seedling survival to sprouting. Others have demonstrated that northern red oak had superior sprouting compared to red maple, sugar maple, American beech, and white ash (Christianson 1971, Swan 1970). Johnson (1974) reported that 40 percent of naturally growing, 2-year-old northern red oak seedlings sprouted following fire. Limitations in these previous studies included:

1) sprouting often could not be separated from survival results, or
2) sprouting was inferred from density or survival results, or
3) studies focused on seedlings (i.e., < 140 cm tall; Christianson 1971, Johnson 1974, Kruger and Reich 1997, Huddle and Pallardy 1999, Brose and Van Lear 1998, Elliott and others 1999).

Saplings (1-10 cm DBH) are more likely than seedlings to replace canopy trees in gaps and after stand removal disturbances for some species (Sander 1971, Loftis 1983, Runkle 1990; but see Schuler and Fajvan 1999).

There is no question that understory northern red oaks can be fire tolerant via sprouting in some conditions. However, we found that top-killed northern red oak saplings did not produce tall, vigorous sprouts. This result demonstrates that northern red oak is not a ubiquitous sprouter in all conditions. Northern red oak's fire tolerance may vary across gradients of site characteristics, forest types, or fire conditions which may explain why this species is fire tolerant in some experiments, but not in others. Our result that northern red oak sprouted in lower proportions than red maple does concur with results from some other studies. Arthur and others (1998) found that after spring fires, red maple sprouts were 3 times more abundant than chestnut oak sprouts and 10 times more abundant than scarlet oak sprouts. Wendel and Smith (1986) reported that red maple sprouted prolifically and northern red oak sprouted poorly following fire. Through a different approach, Clark and his colleagues (Clark and others 1996, Clark and Royall 1996, Clark 1997) cast doubt on the ubiquitous application of the fire and oak hypothesis (but see Abrams and Seischab (1997) for a reply). They demonstrated through fossil pollen and charcoal records that oaks have been prevalent in areas and times with fire intolerant species (i.e., American beech) and during periods of low fire frequency (Clark and others 1996, Clark and Royall 1996). Our work, and that of Clark and his colleagues, suggests that fire alone does not explain the occurrence of oaks, and in particular northern red oak, in some areas.

Incorporating Deer and Gaps Into The Fire and Oak Hypothesis

We found that deer browsing, after prescribed fires, dramatically reduced the proportion of all top-killed saplings that sprouted, reduced diversity of sprouts by an order of magnitude, and greatly altered species composition of sprouters. Only striped maple and red maple produced large sprouts following fire in the presence of deer browsing. Because sprouting is a major mechanism of regeneration in these forests, deer browsing has the potential to alter successional pathways following fire. In fact, in the absence of deer herbivory, striped maple was an intermediate sprouter but dominated the sprouting community in the presence of herbivory. These interactions between fire and deer demonstrate that fire alone does not always control species composition.

Red maple, sugar maple, and witch hazel saplings have been reported to be fire intolerant and have a low occurrence of sprouting following fire (Wright and Bailey 1982, Burns and Honkala 1990, Huddle and Pallardy 1999). However, we found that all three of these species sprouted at or above the mean sprouting response for the community. Red maple saplings were very fire tolerant and sprouted prolifically even in the presence of deer herbivory. This suggests that the increase in red maple abundance in recent decades may be due not to fire suppression but due to red maple's ability to tolerate deer herbivory. Witch hazel was a prolific sprouter, and sugar maple was an intermediate sprouter both in the absence of deer herbivory. Sugar maple is likely to maintain its dominance following fire in the no-deer plots because it was the dominant sapling in the pretreatment community. Previous work on sugar maple and witch hazel attributed poor sprouting post fire to intolerance to fire (Wright and Bailey 1982, Burns and Honkala 1990). Our results suggest that these two species are tolerant to fire but intolerant to deer browsing.

Unlike browsing and fire, gaps did not alter the proportion of top-killed saplings that sprouted. This was surprising considering the number of published studies on the importance of gaps for many different modes of regeneration including seed germination, seedling and sapling growth, the role of epiphytes, and effects of vines (Canham 1985, Lorimer and others 1988, Runkle 1990, Spies and others 1990, Lawton and Putz 1988, Clebsch and Busing 1989, Schnitzer and others 2000). However, the role of gaps in sprouting is largely unstudied. We found that the high-resource levels in gaps did not alter the proportion of top-killed saplings that sprouted for 14 common species in 32 multi-tree gaps. Further, the effects of gaps did not interact with the effects of fire or deer browsing. Lastly, there were no significant species-specific effects of gaps on sprouting response regardless of fire treatment. This study demonstrates that gaps play little role in the initial sprouting responses of top-killed saplings in this system.

IMPLICATIONS FOR MANAGEMENT

In a recent opinion paper, Brose and others (2001) advocated for a wider use of prescribed fire for the management of oak in mixed hardwood stands. Our results demonstrate that prescribed fire can be very detrimental to sprouting of northern red oak saplings in mixed hardwood stands. Furthermore, prescribed fire in the presence of large deer populations prevented all commercial species from producing vigorous, tall sprouts, except red maple. For decades, deer populations have been at historically high levels in many areas in eastern North America and have been adversely impacting understory vegetation (Beals and others 1960, Marquis 1981, Alverson and others 1988, Tilghman 1989). This suggests that our results on the effects of deer browsing may have broad implications. Undoubtedly, some fires do promote oak regeneration especially in some oak dominated communities; however, fires do not always promote northern red oak in mixed hardwood stands. Additional research testing the effects of fire on other eastern deciduous forest types in the context of deer browsing and other factors will likely elucidate mechanisms by which the fire and oak hypothesis operates.

CONCLUSIONS

Our findings only partially support the fire and oak hypothesis. Canopy northern red oaks were fire tolerant (i.e., had 100 percent survival), however, oak saplings were not fire tolerant and did not produce tall, vigorous sprouts following fire. Further, our findings demonstrate that deer browsing following fire can dramatically reduce regeneration via sprouting leading to communities dominated by striped maple. Although some of these specific results may not be generalizable to all regions within the eastern deciduous forest region, they do cast doubt on the ubiquitous application of the fire and oak hypothesis to explain the dominance of oak in some areas. These findings illustrate that prescribed fires in the presence of high deer populations may prevent forest regeneration and likely shift successional trajectories.

ACKNOWLEDGMENTS

The USDA National Research Initiative Competitive Grant 99-35101-7732, Westvaco Corporation, USDA Forest Service Northeast Experiment Station, the Botany In Action program of the Garden Club of Allegany County and the Phipps Conservatory and Botanical Garden, Pittsburgh, PA, and the University of Pittsburgh Environmental Seed Grants Program supported this work. We thank Mary Beth

Adams, Daniel Bunker, Tiffany Knight, Alex Royo, and two anonymous reviewers for comments on various drafts of this manuscript. We thank Mary Beth Adams, Gary Bustemente, Mark Ford, Thomas Schuler, Tim Sherm and Gary Willison of the USDA Forest Service; and Bruce Brennemen, Patrick Keyser, and David McGill of Westvaco Corporation for a tremendous amount of assistance and logistical support. Lastly, we thank the hard work and dedication of many undergraduate field assistants.

LITERATURE CITED

Abrams, M.D. 1992. Fire and the development of oak forests. BioScience. 42: 346-353.

Abrams, M.D. 1998. The red maple paradox. What explains the widespread expansion of red maple in eastern forests? BioScience. 48: 335-364.

Abrams, M.D.; Seischab, F.K. 1997. Does the absence of sediment charcoal provide substantial evidence against the fire and oak hypothesis? Journal of Ecology. 85: 373-375.

Alverson, W.S.; Donald, M.W.; Solheim, S.L. 1988. Forests too deer: edge effects on northern Wisconsin. Conservation Biology. 2: 348-358.

Anderson, R.C.; Loucks, O.L. 1979. White-tail deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. Journal of Applied Ecology. 16: 855-861.

Arthur, M.A.; Paratley, R.D.; Blankenship, B.A. 1998. Single and repeated fires affect survival and regeneration of woody and herbaceous species in an oak-pine forest. Journal of the Torrey Botanical Society. 125: 225-236.

Barden, L.S. 1981. Forest development in canopy gaps of a diverse hardwood forest of the southern Appalachian Mountains. OIKOS. 37: 205-209.

Barden, L.S. 1996. A comparison of growth efficiency of plants on the east and west sides of a forest canopy gap. Bulletin of the Torrey Botanical Club. 123: 240-242.

Beals, E.W.; Cottam, G.; Vogl, R.J. 1960. Influence of deer on vegetation of the Apostle Islands, Wisconsin. Journal of Wildlife Management. 24: 68-80.

Bond, W.J.; Midgley, J.J. 2001. Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology and Evolution. 16: 45-51.

Braun, E.L. 1967. Deciduous forests of eastern North America. New York, NY: Hafner Publishing Company. 596 p.

Brose, P.H.; Schuler, T.; Van Lear, D.; Berst, J. 2001. Bringing fire back: the changing regime of the Appalachian mixed-oak forests. Journal of Forestry. 99: 30-35.

Brose, P.H.; Van Lear, D.H. 1998. Responses of hardwood advance regeneration to seasonal prescribed fire in oak-dominated shelterwood stands. Canadian Journal of Forest Research. 28: 331-339.

Brose, P.H.; Van Lear, D.H. 1999. Effects of seasonal prescribed fires on residual overstory trees in oak-dominated shelterwood stands. Southern Journal of Applied Forestry. 23: 88-93.

Burns, R.M.; Honkala, B.H., tech. coord. 1990. Silvics of North America. Agric. Handb. 654. Volume 2. Hardwoods. Washington, DC: U.S. Department of Agriculture, Forest Service. 877 p.

Butterworth, J.S.; Tzilkowski, W.M. 1990. Understory response to heavy thinning in oak stands with and without deer exclosures. Journal of the Pennsylvania Academy of Science. 64: 81-84.

Canham, C.D. 1985. Suppression and release during canopy recruitment in *Acer saccharum.* Bulletin of the Torrey Botanical Club. 112: 134-145.

Castleberry, S.B.; Ford, W.M.; Miller, K.V.; Smith, W.P. 2000. Influences of herbivory and canopy openings in size on forest regeneration in a southern bottomland hardwood forest. Forest Ecology and Management. 131: 57-64.

Christianson, J.D. 1971. The effect of surface fires on three species of hardwood tree seedlings. The William L. Hutcheson Memorial Forest Bulletin. 2: 1-5.

Clark, J.S. 1997. Facing short-term extrapolation with long-term evidence: holocene fire in the north-eastern US forests. Journal of Ecology. 85: 377-380.

Clark, J.S.; Royall, D. 1996. Local and regional sediment charcoal evidence for fire regimes in presettlement north eastern North America. Journal of Ecology. 84: 365-382.

Clark, J.S.; Royall, P.D.; Chumbley, C. 1996. The role of fire during climate change in an eastern deciduous forest at Devil's Bathtub, New York. Ecology. 77: 2148-2166.

Clebsch, E.E.; Busing, R.T. 1989. Secondary succession, gap dynamics and community structure in a southern Appalachian cove forest. Ecology. 70: 728-735.

Cole, K.L.; Klick, K.F.; Pavlovic, N.B. 1992. Fire temperature monitoring during experimental burns in Indiana Dunes Nation Lakeshore. Natural Areas Journal. 12: 177-183.

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

Delcourt, P.A.; Delcourt, H.R. 1987. Long-term forest dynamics of the temperate zone. New York, NY: Springer-Verlag. 439 p.

Ehrenfeld, J.G. 1980. Understory response to canopy gaps of varying size in a mature oak forest. Bulletin of the Torrey Botanical Club. 107: 29-41.

Elliott, K.J.; Hendrick, R.L.; Major, A.E.; Vose, J.M.; Swank, W.T. 1999. Vegetation dynamics after prescribed fire in the southern Appalachians. Forest Ecology and Management. 114: 199-213.

Ford, W.M.; Johnson, A.S.; Hale, P.E. 1994. Nutritional quality of deer browse in southern Appalachian clearcuts and mature forest. Forest Ecology and Management. 67: 149-157.

Gleason, H.A.; Cronquist, A. 1991. Manual of vascular plants of northeastern United States and adjacent Canada. Bronx, NY: The New York Botanical Garden. 910 p.

Gordon, A.M.; Simpson, J.A.; Williams, P.A. 1995. Six-year response of red oak seedlings planted under a shelterwood in central Ontario. Canadian Journal of Forest Research. 25: 603-613.

Guyette, R.; Dey, D. 1996. A history of fire, disturbance, and growth in a red oak stand in the Bancoft District, Ontario. For. Res. Inf. Pap. 119. Ontario, Canada: Ontario Forest Research Institute. 14 p.

Guyette, R.P.; Dey, D.C. 2000. Humans, topography, and wildlands fire: the ingredients for long-term patterns in ecosystems. In: Yaussy, D.A., ed. Proceedings, Workshop on fire, people and the Central Hardwood landscape. Gen. Tech. Rep. NE-274. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 28-35.

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

Huddle, J.A.; Pallardy, S.G. 1996. Effects of long-term annual and periodic burning on tree survival and growth in a Missouri Ozark oak-hickory forest. Forest Ecology and Management. 82: 1-9.

Huddle, J.A.; Pallardy, S.G. 1999. Effect of fire on survival and growth of *Acer rubrum* and *Quercus* seedlings. Forest Ecology and Management. 118: 49-56.

Johnson, P.S. 1974. Survival and growth of northern red oak seedlings following a prescribed burn. Res. Note NC-177. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 3 p.

Johnson, P.S. 1993. Perspectives on the ecology and silviculture of oak-dominated forests in the central and eastern states. Gen. Tech. Rep. NC-153. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 28 p.

Kitterage, D.B.; Mark, P.; Ashton, S. 1995. Impact of deer browsing on regeneration in mixed stands in southern New England. Northern Journal of Applied Forestry. 12: 115-120.

Kline, V.M.; Cottam, G. 1979. Vegetation response to climate and fire in the driftless area of Wisconsin. Ecology. 60: 861-868.

Kruger, E.L.; Reich, P.B. 1997. Responses of hardwood regeneration to fire in mesic forest openings. I. Post-fire community dynamics. Canadian Journal of Forest Research. 27: 1822-1831.

Lawton, R.O.; Putz, F.E. 1988. Natural disturbance and gap phase regeneration in a wind-exposed tropical cloud forest. Ecology. 69: 764-777.

Littell, R.C.; Freund, R.J.; Spector, P.C. 1993. SAS Systems for Linear Models. Cary, NC: SAS Institute, Inc.

Loftis, D.L. 1983. Regeneration of southern Appalachian mixed hardwood stands with the shelterwood method. Southern Journal of Applied Forestry. 7: 212-217.

Long, Z.T.; Carson, W.P.; Peterson, C.J. 1998. Can disturbance create refugia from herbivores: an example with hemlock regeneration on treefall mounds. Journal of the Torrey Botanical Society. 125: 165-168.

Lorimer, C.G. 1984. Development of red maple understory in northeastern oak forest. Forest Science. 30: 3-22.

Lorimer, C.G. 1985. The role of fire in the perpetuation of oak forests. In: Challenges in oak management and utilization. Madison, WI: University of Wisconsin-Extension: 1-16.

Lorimer, C.G. 1992. Causes of the oak regeneration problem. In: Loftis, D.L.; McGee, C.E., eds. Oak regeneration: serious problems, practical recommendations. Gen. Tech. Rep. SE-84. Knoxville, TN: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 14-39.

Lorimer, C.G.; Frelich, L.E.; Nordheim, E.V. 1988. Estimating gap origin probabilities for canopy trees. Ecology. 69: 778-785.

Marquis, D.A. 1981. Effects of deer browsing on timber production in Allegheny hardwood forests of northwestern Pennsylvania. Res. Pap. NE-475. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station.

Masters, R.E.; Lochmiller, R.L.; Engle, D.M. 1993. Effects of timber harvest and prescribed fire on white-tailed deer forage production. Journal of Wildlife Management. 21: 401-411.

Merritt, C.; Pope, P.E. 1991. The effects of environmental factors, including wildfire and prescribed burning on the regeneration of oaks in Indiana. Agric. Exp. Sta. Bull. West Lafayette, IN: Purdue University, Department of Forestry and Natural Resources. 612 p.

Nyland, R.D.; Abrahamson, L.P.; Adams, K.B. 1982. Use of prescribe fire for regenerating red and white oak in New York. In: Proceedings, Society of American Foresters conference; Cincinnati, OH. Bethesda, MD: Society of American Foresters: 163-167.

Runkle, J.R. 1990. Gap dynamics in an Ohio *Acer-Fagus* forest and speculation on the geography of disturbance. Canadian Journal of Forest Research. 20: 632-641.

Sander, I.L. 1971. Height growth of new oak sprouts depends on size of advance reproduction. Journal of Forestry. 69: 809-811.

Schnitzer, S.A.; Dalling, J.W.; Carson, W.P. 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. Journal of Ecology. 8: 655-666.

Schuler, T.M.; Fajvan, M.A. 1999. Understory tree characteristics and disturbance history of a central Appalachian forest prior to old-growth harvesting. Res. Pap. NE-710. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 12 p.

Sokal, R.R.; Rohlf, F.J. 1995. Biometry. New York, NY: W.H. Freeman and Company. 887 p.

Spies, T.A.; Franklin, J.F.; Klopsch, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. Canadian Journal of Forest Research. 20: 649-658.

Swan, F.R.J. 1970. Post-fire response of four plant communities in south-central New York state. Ecology. 51(6): 1074-1082.

Tilghman, N.G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. Journal of Wildlife Management. 53: 524-532.

Van Lear, D.H.; Watt, J.M. 1992. The role of fire in oak regeneration. In: Loftis, D.L.; McGee, C.E., eds. Oak regeneration: serious problems, practical recommendations. Gen. Tech. Rep. SE-84. Knoxville, TN: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 66-78.

Wendel, G.W.; Smith, H.C. 1986. Effects of a prescribed fire in a central Appalachian oak-hickory stand. NE-RP-594. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station.

White, A.S. 1983. The effects of thirteen years of annual prescribed burning on a *Quercus ellipsoidalis* community in Minnesota. Ecology. 64: 1081-1085.

Wright, H.A.; Bailey, A.W. 1982. Fire ecology: United States and Southern Canada. New York, NY: John Wiley and Sons.

APPENDICES

Appendix Table 1.—*Codes, genus species and authority according to Gleason and Cronquist (1991), and common name for plant species found on the study sites and discussed in the paper*

Species Code	Scientific name	Common name
ACPE	*Acer pensylvanicum* L.	striped maple
ACRU	*Acer rubrum* L.	red maple
ACSA	*Acer sacharrum* Marsh.	sugar maple
BESP	*Betula lenta* L.	birch
BESP	*Betula alleghaniensis* Britton	birch
CASP	*Carya tomentosa* Nutt.	hickory
CASP	*Carya ovata* (Mill.) K. Koch	hickory
FAGR	*Fagus grandifolia* Ehrh.	American beech
FRAM	*Fraxinus americana* L.	white ash
HAVI	*Hamamelis virginiana* L.	witch hazel
LITU	*Liriodendron tulipifera* L.	yellow poplar
MASP	*Magnolia acuminata* L.	magnolia
MASP	*Magnolia fraseri* Walt.	magnolia
OSVI	*Ostrya virginiana* (Mill.) K. Koch	ironwood
OXAR	*Oxydendrum arboreum* (L.) DC.	sourwood
PRSE	*Prunus serotina* Ehrh.	black cherry
QUPR	*Quercus prinus* L.	chestnut oak
QURU	*Quercus rubra* L.	northern red oak
ROPS	*Robinia pseudoacacia* L.	black locust
TIAM	*Tilia americana* L.	basswood
TSCA	*Tsuga canadensis* (L.) Carr.	eastern hemlock

Appendix Table 2.—*Results of a ANOVA with a split-plot, two-way factorial design testing the effects of Fire, No-Deer and Size on canopy tree survival*

Source	df	SS	MS	*F*	*P*	R^2
Model	13	3.0373	0.2336	4.61	0.0001	0.54
Error	50	2.53120	0.0506			
Source	**df**	**Type III SS**	**Type III MS**	***F***	***P***	
Stand	3	0.6902				
Stand x Fire	3	0.4901	0.1634			
Fire	1	0.7653	0.7653	4.68	0.1191	
No-Deer	1	0.0800	0.0800	1.59	0.2130	
Size	1	0.6359	0.6359	12.64	0.0008	
Fire x No-Deer	1	0.0251	0.0251	0.50	0.4833	
Fire x Size	1	0.2531	0.2531	5.03	0.0292	
No-Deer x Size	1	0.0638	0.0638	1.27	0.2652	
Fire x No-Deer x Size	1	0.0336	0.0336	0.336	0.4188	

Appendix Table 3.—*Results of an ANOVA with a split-plot, two-way factorial design testing the effects of Fire, Size, and Species on canopy tree survival*

Source	**df**	**SS**	**MS**	***F***	***P***	**R^2**
Model	21	11.9006	0.5667	5.980	0.0001	0.52
Error	117	11.0888	0.09478			

Source	**df**	**Type III SS**	**Type III MS**	***F***	***P***
Stand	3	2.7215			
Stand x Fire	3	2.2731	0.7577		
Fire	1	1.9076	1.9076	2.52	0.2108
Species[1]	3	0.6667	0.6667	2.34	0.0765
Size[2]	1	1.9379	1.9379	20.45	0.0001
Fire x Size	1	0.5267	0.5267	5.56	0.0201
Fire x Species	3	1.2339	1.2339	4.34	0.0061
Size x Species	3	0.4865	0.4865	1.71	0.1685
Fire x Size x Species	3	0.2691	0.2691	0.95	0.4206

[1] The four species were red maple, sugar maple, American beech, and basswood.

[2] Size class for trees are Small: 10-19.9 cm DBH; and Large: ≥ 20 cm DBH.

Appendix Table 4.—*Results of an ANOVA with a split-plot, two-way factorial design testing the effects of FIRE, GAP, NO-DEER and their interactions on mean proportion of top-killed sapling with sprouts > 1 cm tall*

Source	**df**	**SS**	***F***	***P***	**R^2**
Model	13	1.8262	4.14	0.0001	0.52
Error	50	1.6974			

Source	**df**	**Type III SS**	**Type III MS**	***F***	***P***
Stand	3	0.0377			
Stand x Fire	3	0.8954	0.0298		
Fire	1	0.9643	0.9643	32.31	0.0108
Gap	1	0.0086	0.0086	0.25	0.6158
No-Deer	1	0.7078	0.7078	20.85	0.0001
Fire x Gap	1	0.0513	0.0513	1.51	0.2245
Fire x No-Deer	1	0.0017	0.0017	0.05	0.8227
Gap x No-Deer	1	0.0000	0.0000	0.00	0.9863
Fire x Gap x No-Deer	1	0.0285	0.0285	0.84	0.3636

Appendix Table 5.—*Results of an ANOVA with a split-plot, two-way factorial design testing the effects of FIRE, GAP, NO-DEER and their interactions on mean proportion of top-killed sapling with tall sprouts (> 50 cm tall)*

Source	**df**	**SS**	***F***	***P***	**R^2**
Model	13	3.7702	9.36	0.0001	0.71
Error	50	1.5495			

Source	**df**	**Type III SS**	**Type III MS**	***F***	***P***
Stand	3	0.9751			
Stand x Fire	3	0.0503	0.0168		
Fire	1	1.1822	1.1822	70.47	0.0035
Gap	1	0.0681	0.0681	2.20	0.1444
No-Deer	1	1.6454	1.6454	53.10	0.0001
Fire x Gap	1	0.0640	0.0640	2.06	0.1571
Fire x No-Deer	1	0.1350	0.1350	4.35	0.0420
Gap X No-Deer	1	0.0001	0.0001	0.00	0.9518
Fire x No-Deer x Gap	1	0.0000	0.0000	0.00	0.9588

Appendix Table 6.—*Results of an ANOVA with a split-plot, two-way factorial design testing the effects of FIRE, GAP, SPECIES and their interactions on the mean proportion of top-killed sapling with sprouts > 50 cm tall in the absence of herbivory*

Source	**df**	**SS**	***F***	***P***	**R^2**
Model	25	11.4051	2.89	0.0003	0.51
Error	70	11.0414			

Source	**df**	**Type III SS**	**Type III MS**	***F***	***P***
Stand	3	2.2414			
Stand x Fire	3	0.2769	0.9230		
Fire	1	1.4053	1.4053	15.22	0.0299
Gap	1	0.1717	0.1717	1.09	0.3004
Species[1]	4	2.3222	2.3222	3.68	0.0089
Fire x Gap	1	0.0004	0.0004	0.00	0.9599
Fire x Species	4	2.8111	2.8111	4.46	0.0029
Gap x Species	4	0.4921	0.4921	0.78	0.5420
Fire x Gap x Species	1	0.3740	0.3740	0.59	0.6690

[1] The species included in this analysis were striped maple, red maple, sugar maple, American beech, and black cherry.