A Meta-Analysis of the Fire-Oak Hypothesis: Does Prescribed Burning Promote Oak Reproduction in Eastern North America?

Patrick H. Brose, Daniel C. Dey, Ross J. Phillips, and Thomas A. Waldrop

Abstract: The fire-oak hypothesis asserts that the current lack of fire is a reason behind the widespread oak (*Quercus* spp.) regeneration difficulties of eastern North America, and use of prescribed burning can help solve this problem. We performed a meta-analysis on the data from 32 prescribed fire studies conducted in mixed-oak forests to test whether they supported the latter assertion. Overall, the results suggested that prescribed fire can contribute to sustaining oak forests in some situations, and we identified several factors key to its successful use. Prescribed fire reduced midstory stem density, although this reduction was concentrated in the smaller-diameter stems. Prescribed fire preferentially selected for oak reproduction and against mesophytic hardwood reproduction, but this difference did not translate to an increase in the relative abundance of oak in the advance regeneration pool. Fire equalized the height growth rates of the two species groups. Establishment of new oak seedlings tended to be greater in burned areas than in unburned areas. Generally, prescribed burning provided the most benefit to oak reproduction when the fires occurred during the growing season and several years after a substantial reduction in overstory density. Single fires conducted in closed-canopy stands had little impact in the short term, but multiple burns eventually did benefit oaks in the long term, especially when followed by a canopy disturbance. Finally, we identify several future research needs from our review and synthesis of the fire-oak literature. For. Sci. ■■(■):000–000.

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Throughout eastern North America, mixed-oak (*Quercus* spp.) forests on upland sites are highly valued for many ecological and economic reasons. Generally, these upland forests consist of one or more oak species (black [*Quercus velutina* Lam.], chestnut [*Quercus montana* Willd.], northern red [*Quercus rubra* L.], scarlet [*Quercus coccinea* Muenchh.], and white [*Quercus alba* L.]) dominating the canopy with a mix of other hardwood species in the midstory and understory strata. Despite widespread abundance and dominance of mixed-oak forests, regenerating them is a chronic challenge for land managers throughout eastern North America and they are slowly being replaced by mesophytic hardwoods such as black birch (*Betula lenta* L.), black cherry (*Prunus serotina* Ehrh.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and yellow-poplar (*Liriodendron tulipifera* L.) (Abrams and Downs 1990, Healy et al. 1997, Schuler and Gillespie 2000, Aldrich et al. 2005, Woodall et al. 2008). Many factors contribute to this oak regeneration problem including loss of seed sources, destruction of acorns and seedlings by insects, disease, weather, and wildlife, dense understory shade, competing vegetation, and lack of periodic fire (Crow 1988, Loftis and McGee 1993, Johnson et al. 2009). The implication of the lack of periodic fire as a cause to the oak regeneration problem arises from the fact that many of these oak forests exist, in part, due to past fires, and this relationship has led to the creation of the fire-oak hypothesis (Abrams 1992, Lorimer 1993, Brose et al. 2001, Nowacki and Abrams 2008, McEwan et al. 2011).

The fire-oak hypothesis consists of four parts: (1) periodic fire has been an integral disturbance in the mixed-oak forests of eastern North America for millennia; (2) oaks have several physical and physiological characteristics that allow them to survive at higher rates than their competitors in a periodic fire regime; (3) the lack of fire in the latter 20th century is a major reason for the chronic, widespread oak regeneration problem; and (4) reintroducing fire via prescribed burning will promote oak reproduction. The first three parts are supported by the scientific literature to various degrees. For example, paleo-ecological studies and historical documents indicate that American Indian tribes used fire for numerous reasons (Day 1953, Wilkins et al. 1991, Patterson 2006, Ruffner 2006). Many studies reported the differences between oaks and mesophytic hardwood species (Gottschalk 1985, 1987, 1994, Kolb et al. 1990), and the concomitant decline of fire and increase in mesophytic hardwoods during the early 1900s is evident from fire history research (Shumway et al. 2001, Guyette et al. 2006, Hutchinson et al. 2008, Aldrich et al. 2010). It remains hard to verify the fourth part of the fire-oak hypothesis—that

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prescribed burning promotes oaks—because the results reported in the literature vary widely. Results range from positive (Brown 1960, Swan 1970, Ward and Stephens 1989, Kruger and Reich 1997) to neutral (Teuke and Van Lear 1982, Merritt and Pope 1991, Hutchinson et al. 2005) to negative (Johnson 1974, Wendel and Smith 1986, Loftis 1990, Collins and Carson 2003). This inconsistency among findings suggests that multiple factors drive fire outcomes and the complex relationships among these factors complicate the development of reliable guidelines for prescribed burning of mixed-oak forests.

Despite the variability in study outcomes and lack of specific guidelines for using fire in oaks, land management agencies throughout eastern North America are increasingly using prescribed fire in mixed-oak forests. For example, the oak-dominated national forests of the Ohio River basin (Allegheny, Daniel Boone, Hoosier, Monongahela, Shawnee, and Wayne) all have prescribed fire as part of their respective forest plans and in 2011 conducted 59 burns totaling 7,776 ha (National Interagency Fire Center 2012). The rationale behind these prescribed fires is that they will benefit oaks by increasing the quantity and quality of understory light by reducing midstory stem density, will increase the overall density of oak reproduction, and will improve the relative abundance and height of oak reproduction in the regeneration pool.

This widespread use of prescribed fire in mixed-oak forests without specific guidelines potentially creates problems, i.e., fire may be applied to oak forests not suitable for burning or fire may be withheld from oak forests that would benefit from burning. A meta-analysis of the fire-oak literature would test the final part of the fire-oak hypothesis and provide guidance on how and when prescribed fire is appropriate or is not useful in the regeneration of mixed-oak forests.

Meta-analysis is a systematic review and statistical synthesis of the empirical data contained in the literature on a particular subject (Borenstein et al. 2009, Harrison 2011). In meta-analysis, a common basis or standard for comparing the results of related studies is chosen, the relevant literature is reviewed, and individual publications are selected or rejected based on meeting that predetermined standard. The means, standard deviations, and sample sizes of the selected publications are statistically analyzed; the result is concise findings that are more broadly applicable than the results of the individual publications.

In 2009, we identified a need for a meta-analysis of the fire-oak literature because no large-scale systematic review and synthesis had been done on the subject and there were a sufficient number of published articles, a lack of guidelines specifically for oak forests, and increasing use of prescribed fire in oak forests by land management agencies. For this meta-analysis we posed the following research hypothesis: Fire will disproportionately benefit oak relative to mesophytic tree species. Specifically, we predict the following:

1. Fire will reduce the density of midstory trees of all species.
2. Oak reproduction will basal sprout after prescribed fires at a higher rate than the reproduction of mesophytic hardwood species.
3. The proportion of oak reproduction relative to that of mesophytic hardwood species will increase postfire.
4. Oak reproduction will be at least as tall as the reproduction of mesophytic hardwood species postfire.
5. Density of new oak seedlings (germinants) will increase postfire.

The first three predictions test direct fire effects, whereas the other two address indirect effects in that they are influenced by other factors (shading, seed production, and adequate seedbed). Prediction 2 is short-term (1 or 2 years postburn), whereas the others are longer, depending on the duration of the study. After testing each prediction, we dissect the result, examining the characteristics of the studies contributing to the outcome of that prediction to comprehend why fire produced that effect. Understanding how and why fire promotes oak reproduction will lay the groundwork for developing prescribed burning guidelines for oak forests.

Data and Methods

For this project, we initially formed a pool of fire-oak publications from our personal files and libraries that we could access directly. This collection was supplemented by Internet searches on Web sites such as Google Scholar and Web of Knowledge for fire-oak publications that we did not possess. Finally, we contacted colleagues involved in fire-oak research for unpublished progress reports on active studies and recently accepted manuscripts. These searches resulted in a database of 187 manuscripts from throughout eastern North America.

We then began winnowing the database using three criteria. Our first criterion was whether the publication provided experimental data that addressed at least one of the five test predictions. This step eliminated the fire history and general discussion publications. Our next criterion was whether the publication contained a sufficient replication of fire treatment(s) to permit statistical analysis. Case studies were thereby eliminated. Our last criterion was whether the publication contained a sufficient description of fire behavior (season of burn and fire intensity) and the site (stand density and management history) to help explain the results. Finally, we decided to focus on the prescribed fire projects instead of the individual publications because some of the projects, especially the large, long-term studies, produced multiple publications. Ultimately, we settled on 50 articles/reports from 32 prescribed fire projects conducted in 15 states for this meta-analysis project (Table 1).

Meta-analysis requires the creation of standards or criteria to compare the results of the studies. These standards may be means, rates, or ratios. For this project, we created the following standards to test the predictions using preburn/postburn or burned/unburned data.

1. Midstory reduction: The mean decrease in the density of stems (2.5–28.0 cm dbh) of all species.

Table 1. Publications of the prescribed fire studies used in this meta-analysis project.

Study	Location	State	Publications	Data available
1	Daniel Boone NF	KY	Alexander et al. 2008	R
2	Clemson Forest	SC	Barnes and Van Lear 1998	M
3	Horsepen WMA	VA	Brose and Van Lear 1998, 2004, Brose et al. 1999, Brose 2010	R
4	State Game Land 29	PA	Brose 2012	R
5	Allegheny NF	PA	Brose 2012*	R
6	Clear Creek SF	PA	Brose et al. 2007	R
7	Westvaco Forest	WV	Collins and Carson 2003	M
8	Purdue Forest	IN	Dolan and Parker 2004	R
9	Chilton Creek Tract	MO	Sasseen and Muzika 2004, Dey and Hartman 2005, Fan et al. 2012	R
10	Land/Lakes NRA	KY	Franklin et al. 2003	R
11	Clemson Forest	SC	Geisinger et al. 1989	R
12	Moshannon SF	PA	Brose et al. 2007, Gottschalk et al. 2012	R
13	Red River Gorge	KY	Arthur et al. 1998, Gilbert et al. 2003, Blankenship and Arthur 2006, Green et al. 2010	R/M
14	University of MO Forest	MO	Paulsell 1957, Huddle and Pallardy 1996	M
15	Bankhead NF	AL	McGee 1979, 1980, Huntley and McGee 1981, 1983	R
16	Vinton Furnace EF	OH	Sutherland and Hutchinson 2003, Hutchinson et al. 2005, 2012	R/M
17	Powhatan WMA	VA	Keyser et al. 1996	R
18	Jordan Timberlands	WI	Kruger and Reich 1997	R
19	Dinsmore Woods	KY	Luken and Shea 2000	R
20	Duke Forest	NC	Maslen 1989	R/M
21	Broome County	NY	McGee et al. 1995	R
22	Morgan SF	IN	Merritt and Pope 1991	R/M
23	Schmeeckle Reserve	WI	Reich et al. 1990	R
24	Fernow EF	WV	Schuler et al. 2012	R
25	Ft. Indiantown Gap	PA	Signell et al. 2005	R/M
26	Clemson Forest	SC	Stottlemyer 2011	R
27	University of TN Forest	TN	Thor and Nichols 1973, DeSelm et al. 1991, Stratton 2007	R/M
28	Sumter NF	SC	Teuke and Van Lear 1982	R
29	Green River WMA	NC	Waldrop et al. 2008	R/M
30	Zaleski SF	OH	Albrecht and McCarthy 2006, Iverson et al. 2008, Waldrop et al. 2008	R/M
31	Goodwin SF	CT	Ward and Brose 2004	R
32	Baxter Hollow	WI	Will-Wolf 1991	M

NF, National Forest; WMA, Wildlife Management Area; SF, State Forest; EF, Experimental Forest; NRA, National Recreation Area; R, reproduction; M, midstory.
* Unpublished data on file at the Forestry Sciences Laboratory, Irvine, PA.

2. Differential sprouting: The difference in postfire basal sprouting rates between oak reproduction (<2.5 cm dbh) and those of mesophytic hardwood species.
3. Oak relative abundance: The change in the proportion of oak reproduction in the regeneration pool (<2.5 cm dbh) between the beginning and end of the study.
4. Oak relative height: The height of the oak reproduction compared with that of mesophytic hardwood species at the end of the study.
5. Oak seedling establishment: The increase in the mean number of new oak seedlings during the course of the study.

Generally, each project provided data for three or four of the standards. Nine projects provided data for just one of the standards and only three of the projects provided data for all five standards. Sometimes the publications provided the data for the standard in the format we needed for the meta-analysis. For example, the publications containing mean preburn/postburn oak seedling or midstory stem densities generally had these data in a ready-to-use format for standards 1 and 5, but for standards 2, 3, and 4, we had to do some simple grouping and calculations before conducting the meta-analysis. For these three standards, we made two species groups: oak and mesophytic species. Hickory (*Carya* spp.) was included with oak because these two genera share many silvical characteristics, whereas the mesophytic group included all other hardwoods generally considered to be competitors to oak and potential oak replacements. For the oak sprouting standard (no. 2), we used the preburn and the immediate postburn stem densities to calculate the mean oak basal sprouting rate by dividing the postburn oak stem density by the corresponding preburn density. We did likewise for the mesophytic group and the two basal sprouting rates (oak and mesophytic) were then used in the meta-analysis. For the oak relative abundance standard (no. 3), we divided the preburn oak stem density by the total preburn stem density and did likewise for the oak and total stem densities reported at the end of the study. For the oak height standard (no. 4), we divided the mean oak seedling height at the end of the study by the corresponding height of the mesophytic species.

Once the standards are extracted from the publications or derived from the results, meta-analysis uses them and the corresponding variances and sample sizes to calculate the "effect size," a measure of the magnitude of the effect of that experiment (Borenstein et al. 2009, Harrison 2011). There are several effect size indices and software programs for calculating them. We chose to use the log response ratio (ln R) as this index because it quantifies the proportionate change that results from experimental manipulation and is commonly used for conducting meta-analysis of ecological studies (Osenberg et al. 1997, Hedges et al. 1999) and MetaWin 2.0 software (Rosenberg et al. 1997) for our project. When the effect size (ln R) is positive, then the fire increases the standard, whereas a negative ln R value indicates that fire decreases the standard. An effect size not significantly different from zero indicates that the fire had no discernible effect on the standard. For each standard, once an effect size is calculated, a cumulative effect size (grand mean) is calculated for all studies providing data for that standard.

The effects of a fire on hardwood reproduction or midstory trees are a function of several factors (Brose and Van Lear 2004) and we tested the influence of some of these factors with summary analysis. This procedure is similar to analysis of variance in that the effect sizes and variances of the studies applicable to each factor are sorted into categories and tested by comparing resulting P values to a critical threshold indicating a significant difference between or among categories (Borenstein et al. 2009, Harrison 2011). For our summary analyses, we chose five factors that we considered to be likely influences on the individual and cumulative effect sizes and that were readily available from the literature (Table 2). These factors were status of oak reproduction, season of burn, number of fires, stem size class, and study duration. Each of these factors contained two or three categories, and the studies were assigned to these categories for the summary analyses. Status of oak reproduction was either released or suppressed. Released oak reproduction consisted of oak seedlings or sprouts that were not limited by lack of sunlight. They had been growing in stands treated with a shelterwood release cut or final harvest several years before the prescribed fire. Suppressed oak reproduction was growing in uncut stands. Season of burn was either dormant or growing season. Dormant-season burns occurred between leaf abscission in the autumn and the beginning of leaf expansion of the mesophytic hardwoods the following spring; growing-season fires occurred during the other months. Number of fires referred to how many prescribed burns were conducted during the study (one, two, or more than two). Stem size class was either saplings (2.5–14.0 cm dbh) or poles (15.0–28.0 cm dbh). Study duration was short-term ($\leq$5 years) or long-term ($>$5 years). Not

Table 2. Characteristics of the prescribed fire studies used in this meta-analysis project.

Study	Location	State	Seedling status	Season of burn	No. of fires	Study duration (y)	No. of replicates
1	Daniel Boone NF	KY	Sup	Dor	2	5	3
2	Clemson Forest	SC	Sup	Dor	3	6	3
3a	Horsepen WMA	VA	Rel	Dor	1	10+	3
3b	Horsepen WMA	VA	Rel	Gro	1	10+	6
4	State Game Land 29	PA	Rel	Gro	1	3	2
5	Allegheny NF	PA	Rel	Gro	2	7	4
6	Clear Creek SF	PA	Sup	Gro	1	3	3
7	Westvaco Forest	WV	Sup	Dor	1	3	4
8	Purdue Forest	IN	Sup	Dor	1	2	3
9	Chilton Creek Tract	MO	Sup	Dor	1, 3, 4	5	5
10	Land/Lakes NRA	KY	Sup	Dor	1, 2	2	6
11	Clemson Forest	SC	Sup	Gro	1	2	3
12	Moshannon SF	PA	Sup	Gro	1	5	3
13	Red River Gorge	KY	Sup	Dor	2, 3	10+	3
14	University of MO Forest	MO	Sup	Dor	10+	10+	2
15a	Bankhead NF	AL	Rel	Dor	1	5	3
15b	Bankhead NF	AL	Sup	Dor	1	5	3
16	Vinton Furnace EF	OH	Sup	Dor	2, 4	7	4
17	Powhatan WMA	VA	Rel	Gro	1	2	2
18	Jordan Timberlands	WI	Rel	Gro	2	2	4
19	Dinsmore Woods	KY	Sup	Dor	2, 3	3	2
20	Duke Forest	NC	Rel	Dor	1	8	3
21	Broome County	NY	Sup	Dor	1, 2	10+	2
22	Morgane SF	IN	Sup	Dor	1, 2	5	4
23	Schmeeckle Reserve	WI	Sup	Dor	1	2	4
24	Fernow EF	WV	Sup	Dor	2	9	2
25	Ft. Indiantown Gap	PA	Sup	Dor	3, 4	1	4
26	Clemson Forest	SC	Rel	Gro	1	3	4
27	University of TN Forest	TN	Rel	Dor	10+	10+	6
28	Sumter NF	SC	Sup	Dor	1	2	3
29a	Green River WMA	NC	Rel	Dor	2	5	3
29b	Green River WMA	NC	Sup	Dor	2	5	3
30a	Zaleski SF	OH	Rel	Dor	2	5	3
30b	Zalesk SF	OH	Sup	Dor	2	5	3
31	Goodwin/ SF	CT	Rel	Gro	1	4	2
32	Baxter Hollow	WI	Sup	Dor	1, 2	4	6

NF, National Forest; WMA, Wildlife Management Area; SF, State Forest; EF, Experimental Forest; NRA, National Recreation Area; Rel, Released; Sup, suppressed; Dor, dormant; Gro, growing.

all factors were pertinent to summary analysis of each standard. For our summary analyses, we used random effects models with an α value of 0.05 for determining statistical significance.

Results

Of the 32 prescribed fire projects, 14 provided data on the changes in midstory density (Figure 1). Mean preburn midstory densities were 513 ± 115 stems/ha and mean postfire midstory densities were 234 ± 45 stems/ha, a 54% reduction. Overall, this reduction in stem density was significant; the grand mean was −0.88 ± 0.61 ln R with the log response ratios of the individual studies ranging from −0.06 to −1.94 ln R. Subsequent summary analysis indicated differences in midstory density reduction by size class ($P = 0.008$) and the number of fires ($P = 0.036$). The decrease in stem density was concentrated in the saplings, especially those less than 10 cm dbh, as postburn sapling densities declined by 88% whereas pole densities dropped by only 15%. Of the three fire categories, single fires did not reduce midstory stem density (13% decline), but two fires and more than two fires did, leading to 36 and 71% declines, respectively. It was not possible to test fire season because all 14 projects used dormant-season fires.

Twenty-three prescribed fire projects provided appropriate data to examine the postfire basal sprouting rates of oak and mesophytic reproduction (Figure 2). Postfire basal sprouting rates reported in the studies or calculated from their data ranged from 13 to 96% for oak and from 5 to 85% for mesophytic species. Overall, oak reproduction sprouted postfire at a 32% higher rate than the mesophytic species, resulting in a significant grand mean of 0.421 ln R. Summary analysis found significant differences between the two species groups by fire season ($P = 0.009$) and status of the reproduction ($P = 0.002$). For growing-season fires, oak reproduction sprouted at a 58% higher rate than the mesophytic species, but after dormant-season fires the difference in sprouting rates between the two groups was nearly zero. Similarly, released oak reproduction sprouted at a 56% higher rate than the mesophytic species, whereas suppressed oak reproduction had a 14% greater sprouting rate than the mesophytic species. When these two factors were combined, sprouting rates were 56% higher for released oaks than for the mesophytic species after growing-season fires, 20% higher for released oaks than for the mesophytic species after dormant-season fires, 14% higher for suppressed oaks than for the mesophytic species after dormant-season fires, and 65% lower for suppressed oaks than for the mesophytic species after growing-season fires. No significant differences were found for number of fires.

Twenty-three studies provided suitable data for examining the change in the relative abundance of oak reproduction (Figure 3). Overall, prescribed burning did not significantly change the proportion of oak reproduction in the advance regeneration pool. The grand mean was 0.342 ± 0.393 ln R. Before burning, mean oak abundance was 25.6% of the seedling pool and after burning it was 26.0%. Summary analysis found only one significant difference: oak relative abundance in studies involving growing-season fire and released reproduction was greater than that with

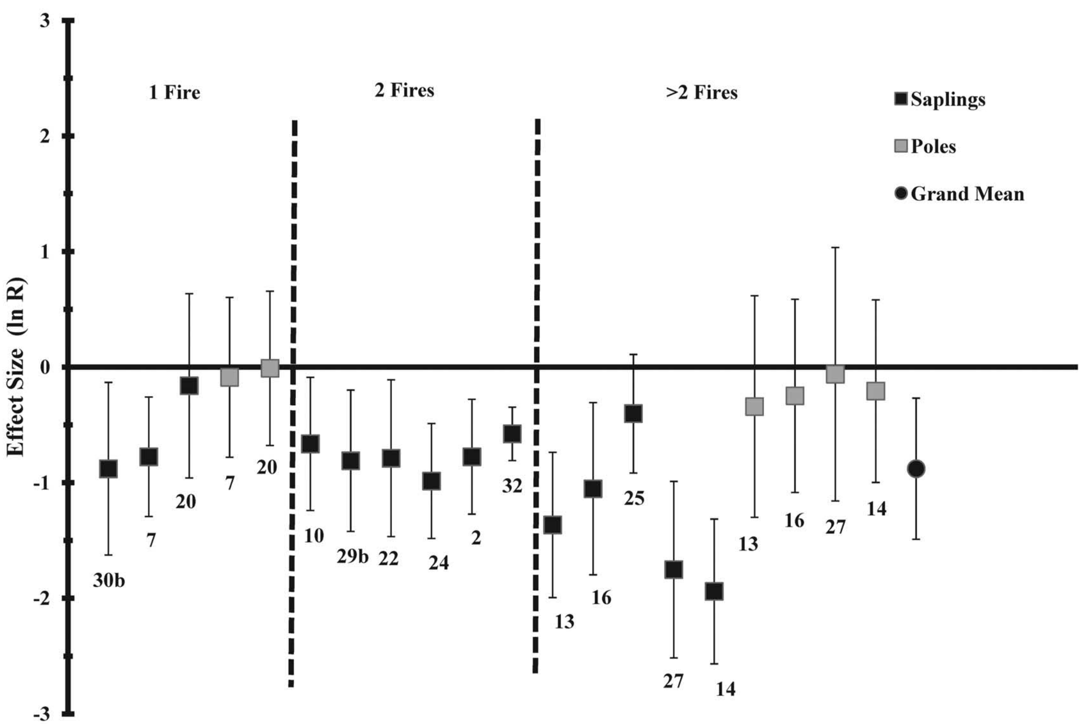

Figure 1. The reduction of pole and sapling stem density (log response ratio ± 95% confidence interval) after prescribed fires conducted throughout the eastern United States. Log response ratios significantly less than zero indicate that the number of midstory stems decreased, whereas log response ratios not different from zero indicate that the postburn densities were unchanged. The numbers refer to the prescribed fire projects in Table 2.

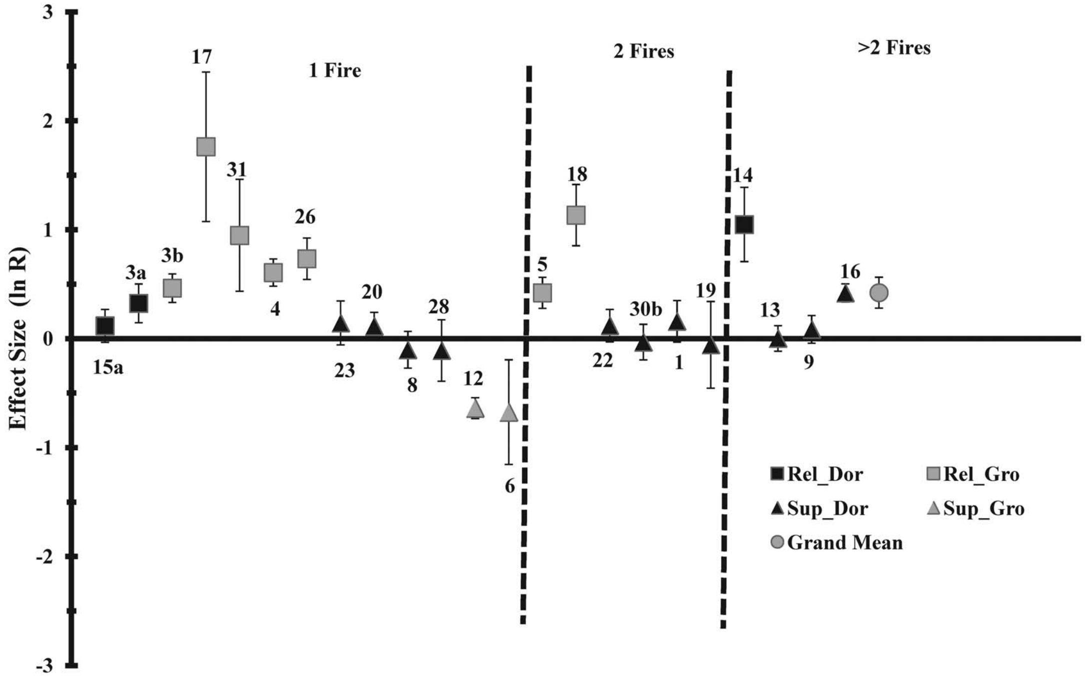

Figure 2. The relative sprouting (log response ratio ± 95% confidence interval) of released (Rel) and suppressed (Sup) oak reproduction in comparison to mesophytic hardwood reproduction following dormant-season (Dor) and growing-season (Gro) prescribed fires conducted throughout the eastern United States. Log response ratios significantly greater than zero indicate that the oak reproduction sprouted postfire at a higher rate than the mesophytic reproduction. Log response ratios significantly less than zero indicate the opposite, and log response ratios not different from zero indicate that the survival rates of the two species groups were equivalent. The numbers refer to the prescribed fire projects in Table 2.

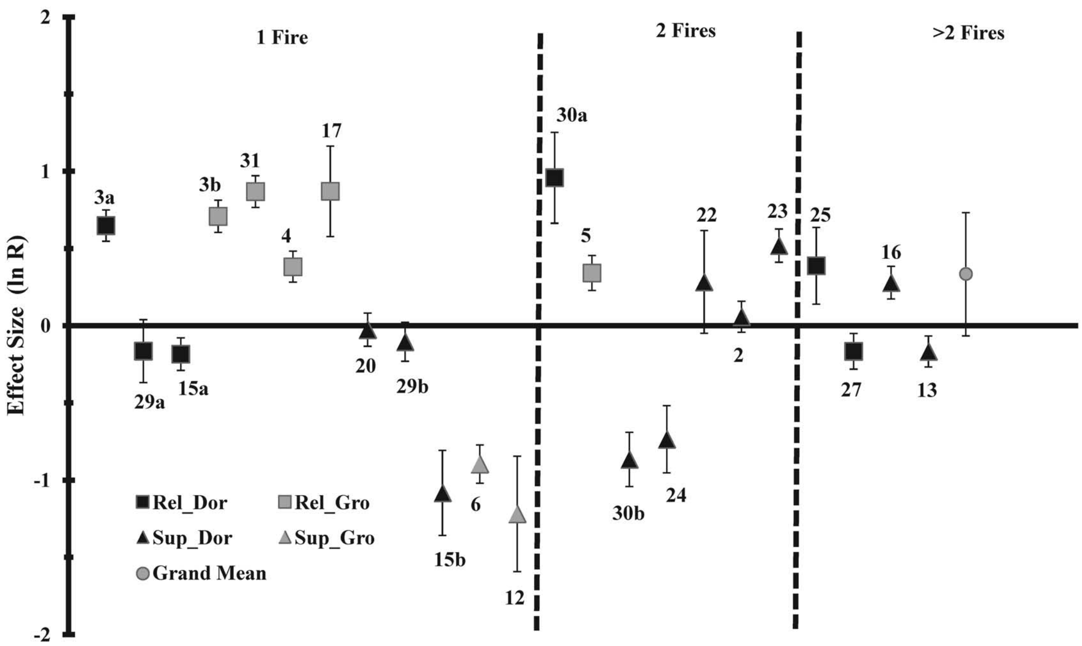

Figure 3. The relative abundance (log response ratio ± 95% confidence interval) of released (Rel) and suppressed (Sup) oak reproduction after dormant-season (Dor) and growing-season (Gro) prescribed fires conducted throughout the eastern United States. Log response ratios significantly greater than zero indicate that the proportion of oak reproduction increased in the regeneration pool. Log response ratios significantly less than zero indicate the opposite, and log response ratios not different from zero indicate that the proportion of oak did not change. The numbers refer to the prescribed fire projects in Table 2.

dormant-season fire and suppressed reproduction (P = 0.006). Otherwise, no differences were found among number of fires (P = 0.873) or between seasons of burn (P = 0.62) or by study duration (P = 0.982).

Only 11 studies provided postburn height data of the oak and mesophytic reproduction (Figure 4). Overall, heights of the oaks were 95% of the heights of the mesophytic species. The grand mean was -0.16 ± 0.18 ln R, indicating no

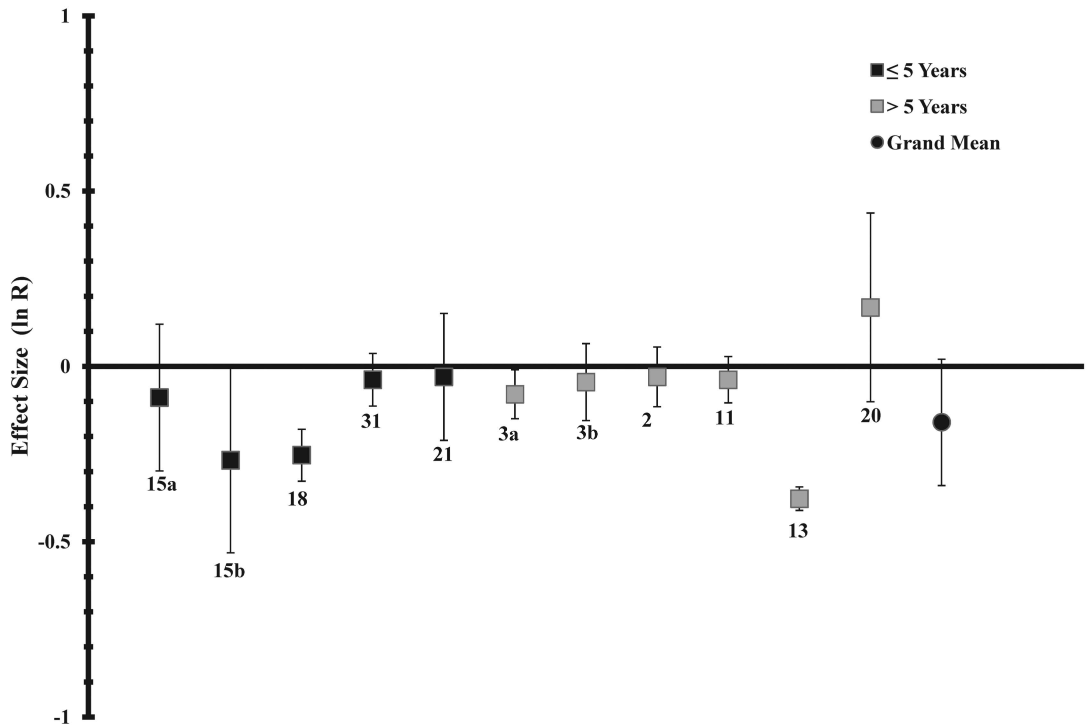

Figure 4. The relative height (log response ratio ± 95% confidence interval) of oak reproduction in comparison to mesophytic hardwood reproduction after short-term (≤5 years) and long-term (>5 years) prescribed fire studies conducted throughout the eastern United States. Log response ratios significantly greater than zero indicate that the oak reproduction was taller than the mesophytic reproduction postfire. Log response ratios significantly less than zero indicate the opposite, and log response ratios not different from zero indicate that the heights of the two species groups were equivalent. The numbers refer to the prescribed fire projects in Table 2.

difference between the two species groups. Summary analysis also found no differences between the categories by season of burn, seedling status, or study duration because their P values ranged from 0.686 to 0.96.

Fifteen fire projects provided data on the establishment of new oak seedlings (Figure 5). Overall, the number of new oak seedlings increased by an average of 1,315 ± 290 stems/ha during the course of these studies, resulting in a grand mean of + 0.33 ln R. This effect size was not different from 0 because of the tremendous variability reported in the studies (individual log response ratios ranged from −1.02 to +0.94). Summary analysis showed no differences based on study duration (P = 0.334).

Discussion

Forestry professionals identify periodic fire as a major reason for the historical occurrence of mixed-oak forests in eastern North America and the cessation of that fire regime in the early 20th century as one of the key factors in the current, widespread oak regeneration problem (Abrams 1992, Brose et al. 2001, Nowacki and Abrams 2008). Consequently, researchers have been engaged in trying to determine how to use prescribed fire to help solve this problem, and their efforts have produced dozens of studies and hundreds of publications replete with examples of when prescribed burning benefited oak reproduction, when it hindered forest renewal, and when it had a negligible impact on the regeneration process. Meta-analysis offers a means by which these divergent studies can be compared on a common basis to support or refute the notion that prescribed fire can help regenerate mixed-oak forests.

Prediction Testing

The results of our meta-analysis support the idea that prescribed fire can help regenerate mixed-oak forests in some situations. Prescribed burning reduced the density of midstory stems (prediction 1), oak reproduction sprouted postfire at higher rates than mesophytic reproduction (prediction 2), and postfire height growth of oak reproduction was comparable to that of mesophytic reproduction (prediction 4). In addition, establishment of new oak seedlings showed a trend toward greater density in burned areas relative to unburned control areas (prediction 5). Collectively and individually, all four of these findings indicate that fire moves an oak forest through the regeneration process in a manner consistent with sustaining that forest's oak component in the future.

Further testing of these predictions and the nonsignificant outcome of prediction 3 (that the postfire proportion of oak reproduction will be greater than that of other hardwood species) illustrate some important caveats on using fire to promote oak regeneration. Reduction of midstory density (prediction 1) was dependent on the diameters of the stems and the number of fires. Single fires, especially those in the dormant season, decreased the number of small saplings, especially those less than 10 cm dbh but had virtually no

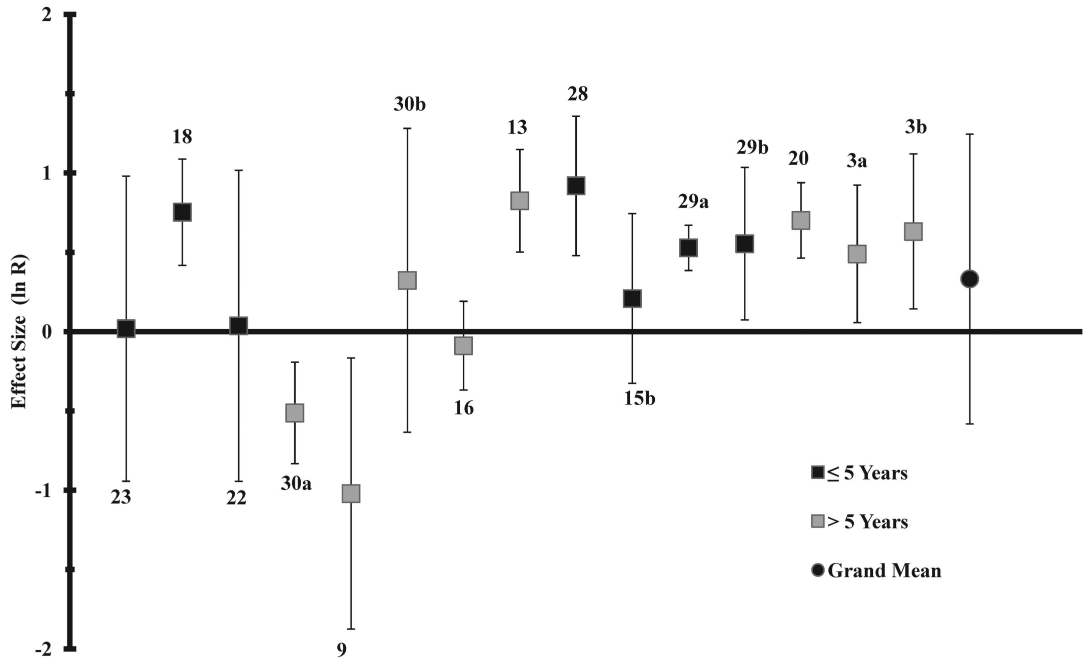

Figure 5. The establishment of new oak seedlings (log response ratio ± 95% confidence interval) after short-term (≤5 years) and long-term (>5 years) prescribed fire studies. Log response ratios significantly greater than zero indicate an increase in the density of new oak seedlings, whereas log response ratios significantly less than zero indicate the opposite, and log response ratios not different from zero indicate no change in the density of new oak seedlings. The numbers refer to the prescribed fire projects in Table 2.

effect on larger diameter stems. This outcome is understandable because prescribed fires are conducted under predetermined fuel and weather conditions to minimize the risk of escape and damage to valuable crop trees. Once hardwoods have grown beyond 10 cm dbh, they are large enough and have thick enough bark to survive most prescribed burning, especially single, low-intensity, dormant-season fires. Multiple fires do eventually cause a reduction in the number of larger saplings and poles. Unfortunately, the multifire data came entirely from dormant-season fires so comparing them with growing-season burns was not possible. However, it is likely that growing-season fires would have a faster and greater impact than dormant-season burns on reducing the density of larger diameter stems.

The superior postfire sprouting ability of oak reproduction (prediction 2) was probably a result of their tendency to allocate carbon more to root development than to stem development in contrast with many of the mesophytic hardwood species (Gottschalk 1985, 1987, 1994, Kolb et al. 1990, Brose 2011). Superior oak sprouting was not universally observed, however; the status of the reproduction (released or suppressed) and fire seasonality (dormant or growing season) were major factors in the outcome. Growing-season fires involving released reproduction produced the largest advantage to oaks in postfire sprouting rates. Conversely, growing-season fires involving suppressed reproduction resulted in a postfire oak sprouting rate *less* than that of the competitors. This was probably the result of the suppressed oak seedlings having smaller roots and depleted carbohydrate reserves relative to the larger, well-established, shade-tolerant mesophytic species. For dormant-season burns, the postfire sprouting rates of oaks were slightly but nonsignificantly higher than those of the competing mesophytic species, regardless of whether the oak reproduction was suppressed or had been released. The few dormant-season studies that showed a difference in sprouting rates between the two species groups had extenuating circumstances such as the competitor's high susceptibility to fire or the use of several burns.

The superior postfire sprouting ability of oak did not translate into an increase in oak's relative abundance in the regeneration pool (prediction 3). Generally, changes in oak relative abundance tended to follow the previously described patterns of oak sprouting. Prescribed growing-season burns involving released oak reproduction resulted in greater oak relative abundance, whereas dormant-season fires or any fires involving suppressed oak reproduction usually showed decreased relative abundance or no appreciable change. The overall lack of change in oak relative abundance is probably a result of new mesophytic seedlings germinating from the seed stored in the forest floor (Schuler et al. 2010) or disseminated from nearby trees or sprouts arising from root systems.

The equalizing of postfire height growth between oak and mesophytic reproduction (prediction 4) should be interpreted cautiously. First, the mesophytic group contained a wide variety of hardwood species, everything other than oak and hickory, so the mean heights used in the meta-analysis were tempered by the slower growing species. Unfortunately, many of the studies did not differentiate well enough among mesophytic species to allow us to focus on primary competitors such as yellow-poplar. Second, height growth of sprouting hardwoods after fire is a function of their prefire size and vigor, the degree of shading, and site quality. The 11 studies used in the meta-analysis represented a diverse mix of prefire seedling conditions, canopy cover, and sites. Thus, the equal height growth of oak and mesophytic reproduction postfire may be an artifact of the inherent variability among the studies rather than a biological certainty that oak reproduction can match mesophyitc reproduction in height growth postfire.

Prediction 5, that fires facilitate the establishment of new oak seedlings, must also be interpreted cautiously. We intended to use only studies that tallied multiple stems arising from the same rootstock as one stem, but sometimes we could not determine from some of the projects whether this was how the reproduction was inventoried. Moreover, only a few of the publications mentioned the occurrence of an acorn crop, an essential precursor to establishment of new oak seedlings. It is not clear whether fires actually improve the germination success of acorns or whether the reported increases were the result of the inventorying procedures.

Management Implications

In even-aged stand management, the regeneration process for mixed-oak forests can last 10 to 25 years depending on numerous factors (Loftis 2004, Johnson et al. 2009). The process consists of three major phases, production of acorns, establishment of oak seedlings from those acorns, and development of those seedlings into competitive-sized oak reproduction, and an event, an adequate, timely release of that reproduction (Loftis 2004). Two intrinsic factors make the process inevitably slow: sporadic acorn production and root-centered seedling growth. In addition, weather, interfering vegetation, wildlife, dense midstory shade, and other factors can slow or stall any of the three phases.

Based on this meta-analysis, prescribed fire appears to fit into two places in the oak regeneration process. The first is at the beginning of the regeneration process as a site preparation tool. The second is near the end of the regeneration process as a release tool. In either case, the first step in using fire is an inventory of the abundance and size of the oak reproduction, overstory conditions, and potential stand renewal obstacles such as competing and interfering vegetation, browsing pressure by white-tail deer (*Odocoileus virginianus*), and site limitations. The inventory may be a comprehensive examination as is done with stand prescription programs such as SILVAH (Brose et al. 2008) or less-intensive assessment of stand conditions. However, it must be done to determine whether there is enough oak reproduction to proceed with stand regeneration. The determination of the adequacy of oak reproduction is highly stand-specific; what is sufficient oak reproduction for one stand may be inadequate for another based on several extenuating factors such as site characteristics, composition of the competing species, and impact of white-tail deer.

Mature, closed-canopy oak stands that lack adequate oak reproduction are at the beginning of the regeneration process. Burning can decrease midstory density, thereby increasing understory light and can reduce the thickness of the forest floor, especially the litter layer, which can be a barrier to germination and seedling establishment (Korstian 1927, Barrett 1931, Carvell and Tryon 1961, Wang et al. 2005). Site preparation burning may also have a negative impact on populations of acorn pests such as weevils (*Curculio* spp.) (Wright 1986, Riccardi et al. 2004) and xerify the upper layers of the soil (Barnes and Van Lear 1998), making it a less hospitable seedbed for mesophytic hardwoods. This approach will probably take a decade or more because the benefits of burning are initially small and multiple burns are needed to create the desired understory conditions. This appears to be especially true with low-intensity fires conducted in the dormant season. In comparing winter and spring burns, Barnes and Van Lear (1998) concluded that three dormant-season fires were needed to equal the impact of one growing-season burn for intermediate-quality sites in the upper Piedmont region of western South Carolina. Regardless of fire seasonality and fire intensity, site preparation burning will probably be a long-term endeavor because oak seedling establishment is dependent on an acorn crop, and masting in oaks can be highly sporadic due to several intrinsic and extrinsic factors. Furthermore, leaf litter re-accumulates within a few years postburn so the benefit of litter reduction is short-lived. Our conclusion is that site preparation is a fair to good use of prescribed fire in oak management, but the time required to achieve satisfactory results may be a major disadvantage. Reducing midstory shade with herbicides (where permitted) may be a more efficient approach with less potential damage to residual canopy trees.

Oak stands with an adequate density of oak reproduction that have received a heavy partial cut or have been completely harvested are well into the regeneration process because the reproduction is no longer limited by shading. In this context, prescribed burning to release the oak reproduction from the competing mesophytic species appears to be an excellent use of fire as long as the competing stems are less than 10 cm dbh. Of the studies included in this meta-analysis, those that occurred in stands that had been partly to completely harvested several years before the fires showed consistently strong positive benefits to the oak component. The oak reproduction survived at a higher rate than the mesophytic competitors, oak relative abundance increased postfire, and the oak sprouts grew at a rate comparable to that of the mesophytic hardwoods. In release burning, fire seasonality and fire intensity matter. The strongest benefits to oak were associated with moderate- to high-intensity growing-season fires. In practical application, when an oak stand has adequate oak reproduction to proceed with the regeneration process, we recommend harvesting the overstory via a two-cut shelterwood sequence or a final removal cut and then burning either between the shelterwood harvests or after the overstory is completely removed. The key is to wait several years after the harvest to burn so that the oak reproduction has adequate time to develop its root system and increase its probability of vigorous sprouting after future burns (Brose 2008, 2011).

Our review of fire-oak literature suggested several special circumstances that may alter or curtail burning plans. One is that prescribed fires can damage and kill overstory trees, some of which may be high-value crop trees. Although this negative effect has been known for years (Nelson et al. 1933, Paulsell 1957, Berry 1969, Wendel and Smith 1986), it is especially true for burning during a shelterwood sequence because of the elevated fuel loads (Brose and Van Lear 1999). In such cases, slash management (lopping, scattering, or removal from the bases of crop trees) is essential to prevent unacceptable losses. Another fire damage caveat is when an oak stand is in the stem exclusion stage of development. Sapling- and pole-size oaks are quite susceptible to fire scarring and subsequent value loss with little change in species composition (Carvell and Maxey 1969, Ward and Stephens 1989, Maslen 1989). Acorns appear to be quite susceptible to fire damage (Auchmoody and Smith 1993), so we advise against burning shortly after an acorn crop if the germinants from those acorns are needed to become oak advance reproduction. A closely related caveat pertains to small oak seedlings. Prescribed fires will kill suppressed oak reproduction, especially growing-season burns. Although this meta-analysis did not examine the influence of seedling size on the outcome of the studies, it was apparent from the few studies with detailed height data that sprouting rate was affected by size. Large oak reproduction sprouted postfire at consistently higher rates than small oak reproduction, especially when the fire occurred in the growing season, and initially larger stems grew taller after burning under any given overstory stocking and burn treatment. Initial diameter and size of oak reproduction are good indicators of its ability to survive fire and are good predictors of future competitive capacity (Brose and Van Lear 2004, Dey and Hartman 2005). Consequently, when the oak component of the regeneration pool is mostly small reproduction, land managers should consider using low-intensity dormant-season burns to minimize losses or opt for other silvicultural practices such as a shelterwood preparatory cut or individual stem herbicide treatments to move the oak stand forward in the regeneration process.

Two nonoak caveats are the presence of invasive species and deer browsing. Some plant species such as the native hay-scented fern (*Dennstaedtia punctilobula*) and the exotic tree of heaven (*Ailanthus altissima*) can spread rapidly after a fire (Rebbeck et al. 2010, Gottschalk et al. 2012) so their presence in or near the burn unit may require preemptive control measures to prevent their spread. Similarly, white-tail deer will be attracted to burned areas and excessive browsing can quickly turn a potential regeneration success into a failure. Potential deer problems should be identified and mitigated before burning.

Future Research Needs

Our collecting and reviewing of the fire-oak literature and our subsequent meta-analysis identified several knowledge gaps that merit research. They are the following:

1. The relationship between fire intensity and postfire sprouting of hardwood reproduction. We had hoped to include fire intensity as one of the contributing factors, but this was not feasible because the studies had widely divergent approaches to measuring this variable. Some simply described fire intensity (cool, hot, or typical for the conditions) or placed it in broad classes (low, moderate, or high) or measured characteristics of the flaming front, but reported them at the stand or treatment level. Despite this variability, it was clear that relationships exist between fire intensity and postfire sprouting of hardwood reproduction. Fire intensity and postfire sprouting need to be measured at the same scale.
2. Fire effects on the establishment of new oak seedlings. Although our meta-analysis suggests that establishment of new oak seedlings increases postfire, we cannot be sure because some studies included in the analysis did not state exactly how the reproduction was inventoried. Research is needed to determine whether fire promotes establishment of new oak seedlings and to verify the sensitivity of acorns to fire.
3. The impacts of fires on other oak ecosystem components. The vast majority of the fire-oak publications we found directly address regeneration concerns, but the fire effects on other ecosystem properties may be important indirect influences on oak reproduction and oak forest health. For example, oaks are ectomycorrhizal, whereas most of the mesophytic species are endomycorrhizal, and shoestring fungus (*Armillaria mellea*) is a common pathogen implicated in oak decline. How does fire affect these fungal communities? In addition, growing-season burns provide excellent control of competing mesophytic hardwoods, but they may adversely affect ground-nesting birds and herpetofauna in the short term via disrupted nesting or direct mortality. Do these short-term losses really occur or do such burns benefit the overall populations in the long-term by creating improved habitat? Knowing the impacts of fire on potentially sensitive species will help managers tailor their burning prescriptions.
4. A comparison of fire with other silvicultural treatments and the sequencing of fire with other silvicultural treatments. The number of oak forests that could benefit from properly applied prescribed fire far exceeds what can be accomplished, even under the best of circumstances. Knowing the tradeoffs between prescribed fire and a fire surrogate such as herbicide application or mechanical site scarification will help foresters match the right tool with the job. Similarly, the exact sequencing of fire with other silvicultural practices merits more research because the more efficient and streamlined the oak regeneration process is, the more likely it is to succeed. Research on treatment efficiency would help managers make wiser use of their limited budgets.

Literature Cited

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

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

ALBRECHT, M.A., AND B.C. MCCARTHY. 2006. Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests. *For. Ecol. Manage.* 226:88–103.

ALDRICH, P.R., G.R. PARKER, J.R. SEVERSON, AND C.H. MICHLER. 2005. Confirmation of oak recruitment failure in Indiana old-growth forest: 75 years of data. *For. Sci.* 51(5):406–416.

ALDRICH, S.R., C.W. LAFON, H.D. GRISSINO-MAYER, G.G. DEWEESE, AND J.A. HOSS. 2010. Three centuries of fire in montane pine-oak stands on a temperate forest landscape. *Appl. Veg. Sci.* 13:36–46.

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

ARTHUR, M.A., R.D. PARATLEY, AND B.A. BLANKENSHIP. 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.

AUCHMOODY, L.R., AND H.C. SMITH. 1993. *Survival of acorns after fall burning*. US For. Serv. Res. Paper NE-678. Northeastern Forest Experiment Station, Broomall, PA. 5 p.

BARNES, T.A., AND D.H. VAN LEAR. 1998. Prescribed fire effects on advanced regeneration in mixed hardwood stands. *So. J. Appl. For.* 22(3):138–142.

BARRETT, L.I. 1931. Influence of forest litter on the germination and early survival of chestnut oak. *Ecology* 12:476–484.

BERRY, F.H. 1969. *Decay in upland oak stands in Kentucky.* US For. Serv. Res. Paper NE-126. Northeastern Forest Experiment Station, Upper Darby, PA. 16 p

BLANKENSHIP, B.A., AND M.A. ARTHUR. 2006. Stand structure over 9 years in burned and fire-excluded oak stands on the Cumberland Plateau, Kentucky. *For. Ecol. Manage.* 225: 134–145.

BORENSTEIN, M., L.V. HEDGES, J.P.T. HIGGINS, AND H.R. ROTHSTEIN. 2009. *Introduction to meta-analysis.* John Wiley & Sons, Chichester, UK. 421 p.

BROSE, P.H. 2008. Root development of acorn-origin oak seedlings in shelterwood stands on the Appalachian Plateau of northern Pennsylvania: 4-year results. *For. Ecol. Manage.* 255:3374–3381.

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

BROSE, P.H. 2011. A comparison of the effects of different shelterwood harvest methods on the survival and growth of acorn-origin oak seedlings. *Can. J. For. Res.* 41:2359–2374.

BROSE, P.H. 2012. Post-harvest prescribed burning of oak stands: An alternative to the shelterwood-burn technique? In *Proc. of the 18th Central hardwoods forest conference.* US For. Ser. Gen. Tech. Rep NRS-. Northern Research Station, Newtown Square, PA. In press.

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

BROSE, P.H., AND D.H. VAN LEAR. 1999. Effects of seasonal prescribed fires on residual overstory trees in oak-dominated shelterwood stands. *So. J. Appl. For.* 23(2):88–93.

BROSE, P.H., AND D.H. VAN LEAR. 2004. Survival of hardwood regeneration during prescribed fires: The importance of root development and root collar location. P. 123–127 in *Proc. of the Upland oak ecology symposium.* US For. Serv. Gen. Tech. Rep. SRS-73. Southern Research Station, Asheville, NC.

BROSE, P.H., D.H. VAN LEAR, AND R. COOPER. 1999. Using shelterwood harvests and prescribed fire to regenerate oak stands on productive upland sites. *For. Ecol. Manage.* 113:124–141.

BROSE, P.H., K.W. GOTTSCHALK, S.B. HORSLEY, P.D. KNOPP, J.N. KOCHENDERFER, B.J. MCGUINNESS, G.W. MILLER, T.E. RISTAU, S.H. STOLESON, AND S.L. STOUT. 2008. *Prescribing regeneration treatments for mixed-oak forests in the mid-Atlantic region*. US For. Serv. Gen. Tech. Rep. NRS-33. Northern Research Station, Newtown Square, PA. 90 p.

BROSE, P.H., G.W. MILLER, AND K.W. GOTTSCHALK. 2007. Re-introducing fire to the oak forests of Pennsylvania: Response of striped maple. P. 67–77 in *Proc. of the 2005 National silviculture workshop.* US For. Serv. Gen. Tech. Rep. PSW-203. Pacific Southwest Research Station, Albany, CA.

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

BROWN, J.H. 1960. The role of fire in altering the species composition of forests in Rhode Island. *Ecology* 41(2) 310–316.

CARVELL, K.L., AND W.R. MAXEY. 1969. Wildfire destroys! *WV Agr. For. Exp. Stat. Bull.* 2(4–5):12.

CARVELL, K.L., AND E.H. TRYON. 1961. The effect of environmental factors on the abundance of oak regeneration beneath mature oak stands. *For. Sci.* 7:98–105.

COLLINS, R.J., AND W.P. CARSON. 2003. The fire and oak hypothesis: Incorporating the influence of deer browsing and canopy gaps. P. 44–60 in *Proc. of the 13th Central hardwoods forest conference.* US For. Serv. Gen. Tech. Rep. NC-234. North Central Research Station, St. Paul, MN.

CROW, T.R. 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*)—A review. *For. Sci.* 34(1):19–40.

DAY, G.M. 1953. The Indian as an ecological factor in the northeastern forest. *Ecology* 34(2):329–346.

DESELM, H.R., E.E.C. CLEBSCH, AND J.C. RENNIE. 1991. Effects of 27 years of prescribed fire on an oak forest and its soils in middle Tennessee. P. 409–417 in *Proc. of the 6th Biennial southern silviculture research conference.* US For. Serv. Gen. Tech. Rep.SE-70. Southeastern Forest Experiment Station, Asheville, NC.

DEY, D.C., AND G. HARTMAN. 2005. Returning fire to Ozark Highland forest ecosystems: Effects on advance regeneration. *For. Ecol. Manage.* 217:37–53.

DOLAN, B.J., AND G.R. PARKER. 2004. Understory response to disturbance: An investigation of prescribed burning and understory removal treatments. P. 285–291 in *Proc. of the Upland oak ecology symposium.* US For. Serv. Gen. Tech. Rep. SRS-73. Southern Research Station, Asheville, NC.

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

FRANKLIN, S.B., P.A. ROBERTSON, AND J.S. FRALISH. 2003. Prescribed burning effects on upland *Quercus* forest structure and function. *For. Ecol. Manage.* 184:315–335.

GEISINGER, D.R., T.A. WALDROP, J.L. HAYMOND, AND D.H. VAN LEAR. 1989. Sprout growth following winter and spring felling with and without summer broadcast burning. P. 91–94 in *Proc. of Pine-hardwood mixtures: A symposium on management and ecology of the type*. US For. Serv. Gen. Tech. Rep. SE-58. Southeastern Forest Experiment Station, Asheville, NC.

GILBERT, N.L., S.L. JOHNSON., S.K. GLEESON, B.A. BLANKENSHIP, AND M.A. ARTHUR. 2003. Effects of prescribed fire on physiology and growth of *Acer rubrum* and *Quercus* spp. seedlings in an oak-pine forest on the Cumberland Plateau, KY. *J. Torrey Bot. Soc.* 130:253–264.

GOTTSCHALK, K.W. 1985. Effects of shading on growth and development of northern red oak, black oak, black cherry, and red maple seedlings I: Height, diameter, and root/shoot ratio. P. 189–195 in *Proc. of the 5th Central hardwoods forest conference.* University of Illinois Press, Urbana-Champaign, IL.

GOTTSCHALK, K.W. 1987. Effects of shading on growth and development of northern red oak, black oak, black cherry, and red maple seedlings. II: Biomass partitioning and prediction. P. 99–110 in *Proc. of the 6th Central hardwoods forest conference.* University of Tennessee Press, Knoxville, TN.

GOTTSCHALK, K.W. 1994. Shade, leaf growth, and crown development of *Quercus rubra*, *Quercus velutina*, *Prunus serotina*, and *Acer rubrum* seedlings. *Tree Physiol.* 14(7):735–749.

GOTTSCHALK, K.W., G.W. MILLER, AND P.H. BROSE. 2012. Advanced oak seedling development as influenced by shelterwood treatments, fern control, deer fencing, and prescribed fire. In *Proc. of the 18th Central hardwoods forest conference.* US For. Ser. Gen. Tech. Rep NRS-. Northern Research Station, Newtown Square, PA. In press.

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

GUYETTE, R.P., D.C. DEY, M.C. STAMBAUGH, AND R.M. MUZIKA. 2006. Fire scars reveal variability and dynamics of eastern fire regimes. P. 20–39 in *Fire in eastern oak forests: Delivering science to land managers.* US For. Ser. Gen. Tech. Rep NRS-P-1. Northern Research Station, Newtown Square, PA.

HARRISON, F. 2011. Getting started with meta-analysis. *Meth. Ecol. Evol.* 2:1–10.

HEALY, W.M., K.W. GOTTSCHALK., R.P. LONG, AND P.M. WARGO. 1997. Changes in eastern forests: Chestnuts are gone, are the oaks far behind? P. 249–263 in *Transactions of the 62nd North American wildlife and natural resources conference.* Wildlife Management Institute, Washington, DC.

HEDGES, L.V., J. GUREVITCH, AND P.S. CURTIS. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80(4):1150–1156.

HUDDLE, J.A., AND S.G. PALLARDY. 1996. Effects of long-term annual and periodic burning on tree survival and growth in a Missouri Ozark oak-hickory forest. *For. Ecol. Manage.* 82:1–9.

HUNTLEY, J.C., AND C.E. MCGEE. 1981. Timber and wildlife implications of fire in young upland hardwoods. P. 56–66 in *Proc. of the 1st Biennial southern silviculture research conference.* US For. Serv. Gen. Tech. Rep. SO-34. Southern Forest Experiment Station, New Orleans, LA.

HUNTLEY, J.C., AND C.E. MCGEE. 1983. Impact of fire on regeneration and wildlife habitat in upland hardwoods. P. 158–162 in *Proc. of the 1982 Society of American Foresters national convention.* Government Printing Office, Washington, DC.

HUTCHINSON, T.F., R.P. LONG., R.D. FORD, AND E.K. SUTHERLAND. 2008. Fire history and the establishment of oaks and maples in second-growth forests. *Can. J. For. Res.* 38: 1184–1198.

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

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

IVERSON, L.R., T.F. HUTCHINSON., A.M. PRASAD, AND M.P. PETERS. 2008. Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern U.S.: 7-year results. *For. Ecol. Manage.* 255:3135–3050.

JOHNSON, P.S. 1974. *Survival and growth of red oak seedlings following a prescribed burn.* US For. Serv. Res. Note. NC-177. North Central Research Station, St. Paul, MN. 6 p.

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

KEYSER, P.K., P.H. BROSE., D.H. VAN LEAR, AND K.M. BURTNER. 1996. Enhancing oak regeneration with fire in shelterwood stands: Preliminary trials. P. 215–219 in *Transactions of the 61st North American wildlife and natural resources conference.* Wildlife Management Institute, Washington, DC.

KOLB, T.E., K.C. STEINER., L.H. MCCORMICK, AND T.W. BOWERSOX. 1990. Growth and biomass partitioning of northern red oak and yellow-poplar seedlings to light, soil moisture and nutrients in relation to ecological strategy. *For. Ecol. Manage.* 38:65–78.

KORSTIAN, C.F. 1927. *Factors controlling germination and early survival of oaks*. Yale Univ. School of Forestry Bull. 19. 115 p.

KRUGER, E.L., AND P.B. REICH. 1997. Responses of hardwood regeneration to fire in mesic forest openings, I: Post-fire community dynamics. *Can. J. For. Res.* 27:1822–1831.

LOFTIS, D.L. 1990. Predicting post-harvest performance of advance red oak reproduction in the southern Appalachians. *For. Sci.* 36(4):908–916.

LOFTIS, D.L. 2004. Upland oak regeneration and management. P. 163–167 in *Proc. of the Upland oak ecology symposium.* US For. Serv. Gen. Tech. Rep. SRS-73. Southern Research Station, Asheville, NC.

LOFTIS, D.L., AND C.E. MCGEE (EDS.). 1993. *Oak regeneration: Serious problems, practical recommendations.* US For. Ser. Gen. Tech. Rep. SE-84. Southeastern Forest Experiment Station, Asheville, NC. 319 p.

LORIMER, C.G. 1993. Causes of the oak regeneration problem. P. 14–39 in *Oak regeneration: Serious problems, practical recommendations.* US For. Ser. Gen. Tech. Rep. SE-84. Southeastern Forest Experiment Station, Asheville, NC.

LUKEN, J.O., AND M. SHEA. 2000. Repeated prescribed burning at Dinsmore Woods State Nature Preserve (Kentucky, USA): Responses of the understory community. *Nat. Areas J.* 20(2):150–158.

MASLEN, P. 1989. Response of immature oaks to prescribed fire in the North Carolina Piedmont. P. 259–266 in *Proc. of the 5th Biennial southern silviculture research conference.* US For. Serv. Gen. Tech. Rep. SE-34. Southeastern Forest Experiment Station, Asheville, NC.

MCEWAN, R.W., J.M. DYER, AND N. PEDERSON. 2011. Multiple interacting ecosystem drivers: Toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography* 34:244–256.

MCGEE, C.E. 1979. Fire and other factors related to oak regeneration. P. 75–81 in *Proc. of the John S. Wright forestry conference.* Purdue University, West Lafayette, IN.

MCGEE, C.E. 1980. The effect of fire on species dominance in young upland hardwood stands. P. 97–104 in *Proc. of the Mid-south upland hardwood symposium.* US For. Serv. Tech. Rep. SA-TP-12. Southeastern Area State and Private Forestry, Atlanta, GA.

MCGEE, G.G., D.J. LEOPOLD, AND R.D. NYLAND. 1995. Understory response to springtime prescribed fire in two New York transition oak forests. *For. Ecol. Manage.* 76:149–168.

MERRITT, C., AND P.E. POPE. 1991. *The effect of environmental factors, including wildfire and prescribed burning, on the regeneration of oaks in Indiana*. Purdue University Agricultural Experiment Station Bulletin No. 612. 45 p.

NATIONAL INTERAGENCY FIRE CENTER. 2012. Wildfire and prescribed fire summary statistics for 2011. Available online at www.nifc.gov/fireInfo/fireInfo_statistics.html. Last accessed June 3, 2012.

NELSON, R.M., I.H. SIMS, AND M.S. ABELL. 1933. Basal fire wounds on some southern Appalachian hardwoods. *J. For.* 31:829–837.

NOWACKI, G.J., AND M.D. ABRAMS. 2008. The demise of fire and the mesophication of forests in the eastern United States. *BioScience* 58(2) 123–138.

OSENBERG, C.W., O. SARNELLE, AND S.D. COOPER. 1997. Effect size in ecological experiments: The application of biological models in meta-analysis. *Am. Nat.* 150(6):798–812.

PATTERSON, W.A. 2006. The paleoecology of fire and oaks in eastern forests. P. 2–19 in *Fire in eastern oak forests: Delivering science to land managers.* US For. Ser. Gen. Tech. Rep NRS-P-1. Northern Research Station, Newtown Square, PA.

PAULSELL, L.K. 1957. Effects of burning on Ozark hardwood timberlands. University of Missouri Agricultural Experiment Station Bull. No. 640. 24 p.

REBBECK, J., T. HUTCHINSON, L. IVERSON, D. YAUSSY, R. BOYLES, AND M. BOWDEN. 2010. Studying the effects of management practices on *Ailanthus* populations in oak forests. P. 50–51 in *USDA research forum on invasive species.* US For. Ser. Gen. Tech. Rep NRS-P-75. Northern Research Station, Newtown Square, PA.

REICH, P.B., M.D. ABRAMS., D.S. ELLSWORTH, E.L. KRUGER, AND T.J. TABONE. 1990. Fire affects ecophysiology and community dynamics of central Wisconsin oak forest regeneration. *Ecology* 71(6):2179–2190.

RICCARDI, C.L., B.C. MCCARTHY, AND R.P. LONG. 2004. Oak seed populations, weevil (Coleoptera: Curculionidae) populations, and predation rates in mixed-oak forests in southeast Ohio. P. 10–20 in *Proc. of the 14th Central hardwood forest conference.* US For. Ser. Gen. Tech. Rep. NE-316. Northeastern Forest Experiment Station, Newtown Square, PA.

ROSENBERG, M.S., D.C. ADAMS, AND J. GUREVITCH. 1997. *Metawin: Statistical software for meta-analysis.* Sinauer Associates, Sunderland, MA. 133 p.

RUFFNER, C.M. 2006. Understanding the evidence for historical fire across eastern forests. P. 40–48 in *Fire in eastern oak forests: Delivering science to land managers.* US For. Ser. Gen. Tech. Rep NRS-P-1. Northern Research Station, Newtown Square, PA.

SASSEEN, A.N., AND R.M. MUZIKA. 2004. Timber harvesting, prescribed fire, and vegetation dynamics in the Missouri Ozarks. P. 179–192 in *Proc. of the 14th Central hardwood forest conference.* US For. Ser. Gen. Tech. Rep. NE-316. Northeastern Forest Experiment Station, Newtown Square, PA.

SCHULER, T.M., AND A.R. GILLESPIE. 2000. Temporal patterns of woody species diversity in a central Appalachian forest from 1856 to 1997. *J. Torrey Bot. Soc.* 127(2):149–161.

SCHULER, T.M., M. THOMAS-VAN GUNDY, M.B. ADAMS, AND W.M. FORD. 2010. Seed bank response to prescribed fire in the central Appalachians. US For. Ser. Res. Pap. NRS-RP-9. Northern Research Station, Newtown Square, PA. 9 p.

SCHULER, T.M., M. THOMAS-VAN GUNDY, M.B. ADAMS, AND W.M. FORD. 2012. Analysis of two pre-shelterwood prescribed fires in a mesic mixed-oak forest in West Virginia. In *Proc. of the 18th Central hardwoods forest conference.* US For. Ser. Gen. Tech. Rep NRS-. Northern Research Station, Newtown Square, PA. In press.

SHUMWAY, D.L., M.D. ABRAMS, AND C.M. RUFFNER. 2001. A 400-year history of fire and oak recruitment in an old-growth oak forest in western Maryland. *Can. J. For. Res.* 31:1437–1443.

SIGNELL, S.A., M.D. ABRAMS., J.C. HOVIS, AND S.W. HENRY. 2005. Impact of multiple fires on stand structure and tree regeneration in central Appalachian oak forests. *For. Ecol. Manage.* 218:146–158.

STOTTLEMYER, A.D. 2011. *Ecosystem responses to fuel reduction treatments in stands killed by southern pine beetle.* Ph.D. dissertation, Clemson Univ., Clemson, SC. 184 p.

STRATTON, R.L. 2007. *Effects of long-term late winter prescribed fire on forest stand dynamics, small mammal populations, and habitat demographics in a Tennessee oak barrens.* M.S. thesis, Univ. of Tennessee, Knoxville, TN. 89 p.

SUTHERLAND, E.K., AND T.F. HUTCHINSON. 2003. Characteristics of mixed-oak forest ecosystems in southern Ohio prior to the reintroduction of fire. US For. Serv. Gen. Tech. Rep. NE-299. Northeastern Forest Experiment Station, Newtown Square, PA. 159 p.

SWAN, F.R. 1970. Post-fire response of four plant communities in south-central New York State. *J. Ecol.* 51(6):1074–1082.

TEUKE, M.J., AND D.H. VAN LEAR. 1982. *Prescribed burning and oak advance regeneration in the southern Appalachians*. Georgia Forestry Commission Res. Paper No. 30. 11 p.

THOR, E., AND G.M. NICHOLS. 1973. Some effects of fires on litter, soil, and hardwood regeneration. P. 317–329 in *Proc. of the 13th Tall Timbers fire ecology conference.* Tall Timbers Research Station, Tallahassee, FL.

WALDROP, T.A., D.A. YAUSSY., R.J. PHILLIPS, T.F. HUTCHINSON, L. BRUDNAK, AND R.E.J. BOERNER. 2008. Fuel reduction treatments affect stand structure of hardwood forests in western North Carolina and southern Ohio, USA. *For. Ecol. Manage.* 255:3117–3129.

WANG, G.G., D.H. VAN LEAR, AND W.L. BAUERLE. 2005. Effects of prescribed fires on first-year establishment of white oak (*Quercus alba* L.) seedlings in the upper Piedmont of South Carolina, USA. *For. Ecol. Manage.* 213:328–337.

WARD, J.S., AND P.H. BROSE. 2004. Mortality, survival, and growth of individual stems after prescribed burning in recent hardwood clearcuts. P. 193–199 in *Proc. of the 14th Central hardwoods forest conference.* US For. Serv. Gen. Tech. Rep. NE-316. Northeastern Forest Experiment Station, Newtown Square, PA.

WARD, J.S., AND G.R. STEPHENS. 1989. Long-term effects of a 1932 surface fire on stand structure in a Connecticut mixed hardwood forest. P. 267–273 in *Proc. of the 7th Central hardwoods forest conference.* US For. Serv. Gen. Tech. Rep. NC-132. North Central Forest Experiment Station, St. Paul, MN.

WENDEL, G.W., AND H.C. SMITH. 1986. *Effects of a prescribed fire in a central Appalachian oak-hickory stand.* US For. Serv. Res. Paper NE-594. Northeastern Forest Experiment Station, Broomall, PA. 8 p.

WILKINS, G.R., P.A. DELCOURT., H.R. DELCOURT, F.W. HARRISON, AND M.R. TURNER. 1991. Paleoecology of Kentucky since the last glacial maximum. *Quat. Res.* 36:224–239.

WILL-WOLF, S. 1991. Role of fire in maintaining oaks in mesic oak maple forests. P. 27–33 in *Proc. of the Oak resource of the upper Midwest conference.* University of Minnesota Extension Service. Minneapolis, MN.

WOODALL, C.W., MORIN, R.S., STEINMAN, J.R., AND C.H. PERRY. 2008. Status of oak seedlings and saplings in the northern United States: Implications for sustainability of oak forests. P. 535–542 in *Proc. of the 16th Central hardwoods forest conference.* US For. Ser. Gen. Tech. Rep. NRS-P-24. Northern Research Station, Newtown Square, PA.

WRIGHT, S.L. 1986. Managing insects affecting oak regeneration by prescribed burning. P. 186–192 in *Current topics in forest research: Emphasis on contributions by woman scientists.* US For. Ser. Gen. Tech. Rep. SE-46. Southeastern Forest Experiment Station, Asheville, NC.