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# Establishment and growth of oak (*Quercus alba*, *Quercus prinus*) seedlings in burned and fire-excluded upland forests on the Cumberland Plateau

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ABSTRACT

Recurrent problems with regeneration of oaks (*Quercus* spp.) have been documented across a wide range of ecosystems. In oak-dominated forests of the central and Appalachian hardwood regions of the United States, a lack of competitive oak regeneration has been tied, in part, to fire suppression in these landscapes, and managers throughout the region are using prescribed fire to address this concern. To examine fire effects on oak regeneration, researchers have generally relied on inventories or population studies of existing seedlings. These studies are valuable but do not permit examination of the role of fire in enhancing the establishment and growth of new oak seedlings stemming from oak mast events. In this study, white (*Quercus alba*) and chestnut oak (*Quercus prinus*) acorn mast crops serendipitously occurred in year three (fall 2005) of a landscape-scale prescribed fire experiment. We examined establishment, survival, height and diameter of new seedlings on sites on the Cumberland Plateau in eastern Kentucky. Treatments were fire exclusion, a single prescribed fire (1x-burn; 2003), and repeated prescribed fire (3x-burn; 2003, 2004, and after acorn drop in 2006), all conducted in late spring. Initial densities of newly established chestnut and white oak seedlings were statistically similar across treatments ($P = 0.42$), despite fires on the 3x-burn site having occurred after acorns were on the ground. Oak seedling density was significantly predicted by oak basal area on all sites ($R^2 = 0.12–0.46$), except for chestnut oak on fire-excluded sites ($R^2 = 0.04$). Litter depth was less on 3x-burn sites compared to 1x-burn and fire-excluded sites, whereas canopy openness was greater on both burn treatments compared to fire-excluded sites. Seedling mortality was generally higher on fire-excluded sites compared to burn sites, especially for white oak. Oak seedling mortality in the first two growing seasons was significantly predicted by initial litter depth and open sky, with greater litter depth and lower percent open sky leading to higher mortality. In the third growing season none of the measured variables predicted chestnut oak seedling survival; for white oak, percent open sky remained a significant predictor of mortality. Initially, seedlings on the fire-excluded sites had similar height but smaller diameter; after three growing seasons there were few differences in seedling height or diameter among treatments. Our findings suggest a potential role for prescribed fire in establishing forest floor and light conditions that may enhance the success of new oak germinants, although different responses among species may suggest the need to target management for individual oak species.



## 1. Introduction

In a variety of ecosystems throughout the world, including temperate deciduous forests, chaparrals, savannahs, and broadleaf evergreen forests, oaks (*Quercus* spp.) are present and often dominant (Johnson et al., 2002). In many of these ecosystems, problems with oak regeneration exist, a result of natural barriers to one or more stages of the complex process of regeneration that includes acorn production and germination, seedling establishment and development, and ultimately, recruitment into the canopy. Alterations to the disturbance regime can also impact the process of oak regeneration, and in some ecosystems, where light availability is central to oak seedling development and recruitment into the canopy, suppression of fire may be a key process limiting successful oak regeneration.

In the eastern hardwood region of North America, oak (*Quercus* spp.) and fire have co-occurred on the landscape for thousands

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of years (Delcourt et al., 1998), with anthropogenic fires in the Cumberland Plateau of Kentucky dating back at least 4000 years (Delcourt and Delcourt, 1997). Recent dendroecological evidence suggests that oaks currently dominating the overstory in upland forests throughout the Cumberland and Alleghany Plateaus established during a period of frequent surface fires (McEwan et al., 2007). Additionally, present day oak-dominated stands originated in a period that was heavily impacted by logging and grazing (Abrams, 1992). Other disturbances in the early 1900s include the American chestnut blight and the extirpation of the passenger pigeon (Ellsworth and McComb, 2003), both of which have been hypothesized to have had an influence on forest composition.

Although oaks dominate the overstory of many eastern deciduous forests (Moser et al., 2006), oak regeneration following the application of a broad range of silvicultural regeneration treatments, over a broad range of sites, has often been insufficient to result in oak stocking consistent with that of the parent stand (Beck and Hooper, 1986; Johnson et al., 2002; Loftis, 1983; Lorimer, 1993; McGee, 1975). There are a multitude of biotic and abiotic factors that result in poor oak regeneration. For example, many present day oak-dominated or mixed-hardwood forests in the eastern US have been without recent major disturbances and thus have maintained relatively closed-canopy status for decades, limiting the potential for oak seedlings in relatively shaded understories to develop (Loftis, 1990a), and harvesting treatments in contemporary oak-dominated stands have not consistently yielded sufficient oak regeneration to stock future stands with oaks (Steiner et al., 2008). Effective fire suppression since the 1930s has exacerbated the lack of oak regeneration by contributing to increased density and size of fire-intolerant species in the midstory (Abrams, 1998; Nowacki and Abrams, 2008). Additional reasons for poor oak regeneration may be partially site-specific. For example, implementation of soil scarification when abundant acorns are present has been used to successfully increase white oak seedling densities and reduce midstory densities of sugar maple (Lhotka and Zaczek, 2003), suggesting that forest floor accumulation impedes oak seedling establishment. A small body of research directly examines the influence of forest litter on the germination and establishment of oak species in the central and Appalachian hardwood forest regions (Barrett, 1931; Kostel-Hughes et al., 2005; Stringer and Taylor, 1999; Wang et al., 2005), and suggests that fire may be effective in reducing the litter layer with positive results for oak seedling establishment. For example, Wang et al. (2005) found that fire increased the establishment of new white oak seedlings by reducing the litter layer and increasing light availability, but found no effects on seedling survival after 1 year.

Forest managers are increasing the use of prescribed fire in Appalachian forests to restore fire as an ecosystem disturbance (Waldrop and Brose, 1999; Welch et al., 2000), often with a common expectation that prescribed fire will enhance oak regeneration (Brose et al., 2001). Yet many short-term studies (1–9 years) examining the effects of single or multiple (up to 4) prescribed fires have resulted in neutral or negative consequences for oak regeneration compared to non-oak competitors (Albrecht and McCarthy, 2006; Alexander et al., 2008; Franklin et al., 2003; Green et al., 2010; Hutchinson et al., 2005; Kuddes-Fischer and Arthur, 2002; Loftis, 1990a). A possible explanation for these results is that oak seedlings and saplings established under closed-canopy forests suffer from low vigor and are incapable of responding to disturbance. Indeed, an exception to these findings was found by Iverson et al. (2008), where oak advance regeneration increased on dry and intermediate sites after canopy thinning followed by at least two fires, a scenario in which the effect of fire on oak seedling success may be somewhat subordinate to the opening of the canopy by thinning. Several studies suggest the importance of size of oak advance reproduction as an important determinant of growth and the likelihood of competing successfully after release (Loftis, 1990b; Sander, 1972; Sander et al., 1984). This is potentially problematic, because large oak advance reproduction does not frequently occur in mature closed-canopy forests (Van Lear et al., 2000). Furthermore, there is evidence that many oak seedlings in the understories of mature oak-dominated forests may be more than a decade old, and some may not respond to modest increases in light resulting from treatments, and are otherwise unable to compete effectively with other seedlings upon canopy release (Dillaway et al., 2007). If some of the oak regeneration pool established under nearly closed canopies does not respond effectively to increased light, perhaps oak seedlings established in recently disturbed areas will demonstrate improved competitive status for future stand replacement. Management to improve the status of oak regeneration may require shifting the focus away from reliance on the current advance regeneration pool established under closed-canopy forests towards approaches to increasing the recruitment of new oak seedlings.

In 2002, a landscape-scale study was initiated to study the effects of prescribed fire on fuels, stand structure, and oak regeneration. A mast crop from white oak (*Quercus alba* L.) and chestnut oak (*Q. prinus* L.) occurred serendipitously in 2005, on sites spanning three pre-existing treatments: fire-excluded, 1x-burn (fire applied in 2003), and 3x-burn (fire applied in 2003, 2004, and then just after the oak mast event, in 2006), providing us with varied combinations of litter depth and canopy openness across our treatment areas. The primary objective of this study was to examine the factors that influence: (1) seedling establishment, (2) seedling survival over three growing seasons, and (3) seedling growth of newly established white and chestnut oak seedlings.

## 2. Methods

### 2.1. Site description

The study area is located in eastern Kentucky on the Cumberland District of the Daniel Boone National Forest in the Cumberland Plateau physiographic region described by Braun (1950). The climate is humid temperate with mean annual precipitation of 114–124 cm and mean annual frost-free days from 160 to 175 (Woods et al., 2002). Geologic substrate varies from the valleys to the ridge tops, with the lower slopes consisting of shales, siltstones, and dolomitic limestones from the Mississippian Borden formation, and upper slopes consisting of shales, siltstones, and sandstones from the Lower Pennsylvanian series (Philley, 1978). Soils are unglaciated, primarily from the Berks–Cranston–Latham association, originating from shale and siltstone parent material (Avers et al., 1974). Forest stands are second growth, approximately 80 years old, with oak site index ranging from SI = 50 to SI = 100. Oak and hickory (*Carya* spp.) dominate the overstory (stems $\geq$10 cm diameter at breast height (DBH)), which had pre-burn basal area of 20–30 $m^2$ $ha^{-1}$. In the midstory (trees 2–10 cm DBH), maple (*Acer rubrum* L. and *Acer saccharum* Marsh.) comprised 45% of stem density; oak relative density in the midstory was <3% (Green, 2005). Seedlings less than 0.6 m height, including germinants, were dominated by maples (7550 stems/ha) and sassafras (*Sassafras albidum* (Nutt.) Nees) (3950/ha), followed by oaks (3450/ha) and hickories (906/ha).

### 2.2. Experimental design

Three study sites, Buck Creek, Chestnut Cliffs and Wolf Pen, were located within an 18 $km^2$ area in Bath and Menifee counties, each ranging in size from 200 to 300 ha. Each study site had three treatment areas established in 2002: fire-excluded, infrequent prescribed fire (fire prescribed in 2003 and hereafter referred to as '1x-burn'), and frequent prescribed fire (fire prescribed in 2003, 2004, and 2006, hereafter referred to as '3x-burn'). In the 3x-burn sites, fire was applied in 2006 despite the presence of new seedlings to meet obligations to the funding agency for maintaining the original experimental design. Fire was also applied to the 3x-burn sites in 2008, but data on seedling mortality after the 2008 burn are not included in data analysis or presentation. We did include diameter and height data from seedlings on the 3x-burn site that survived the 2008 prescribed fire. Each treatment area contained 8–12 plots, each 10 m × 40 m, arrayed parallel to the topographic contour for a total of 93 plots.

USDA Forest Service staff from the Cumberland Ranger District of the Daniel Boone National Forest conducted the prescribed fires, all of which were late-dormant season or early growing season burns (from late March to mid-April) of low to moderate intensity. Detailed information on burn conditions can be found in Alexander et al. (2008). A wildfire occurred on the Wolf Pen fire-excluded site in December 2006 that affected 5 plots. These plots were eliminated from all analyses that included data from sampling periods from May 2007 onward; data from these plots that predate the wildfire were retained.

As part of the larger research project to study the effects of prescribed fire, data on stand structure were collected in each of the 93 plots. All trees ≥10 cm DBH were identified to species and DBH measured. Basal area (BA) of white oak and chestnut oak ≥10 cm DBH reported in this study are based on stand data collected in 2004.

### 2.3. Oak seedling establishment and growth

Following white and chestnut oak mast events in fall 2005, we sampled oak seedling establishment in May 2006. Pre-planned prescribed fires in 'frequent' burn sites were conducted in April 2006 as part of the ongoing study. Belt transects 20 m × 1 m were established, located 2 m above and below each main plot, parallel to the long axis of the main plot. All first year oak seedlings observed within each transect were tagged with a unique number. Only oak seedlings that had an acorn attached or evidence of cotyledon remnants were marked, and the litter depth of the seedling location was recorded to the nearest 0.5 cm.

There were a total of 3483 new oak seedlings marked in May 2006 on 76 of the 93 sample plots; 17 plots had no new seedlings in the two transect locations. The white oak group (section *Leucobalanus*) represented 99% of new seedlings (white oak 53%, chestnut oak 46%); only 1% of the new oak seedlings were in the red oak group (section *Erythrobalanus*). Of the 76 plots with new oak seedlings, five had seedlings only in the red oak group; thus the sample population of seedlings in the white oak group were found in a total of 71 plots, and because of the predominance of new seedlings in the white oak group across the study area, only those 71 plots are included in this study.

Seedlings were monitored for survival three times, in August 2006, 2007, and 2008. Stem height was also measured in August 2006, 2007, and 2008. Stem height was measured to the nearest 0.1 cm from the root collar to the terminal bud. Basal diameter was recorded in August 2007 and 2008. Two basal diameter measurements (perpendicular to each other) were taken for each live seedling with digital calipers 0.5 cm above the root collar. This protocol was established for two reasons: (1) the root collar often had either an attached acorn or cotyledon remnants which we did not want to damage; and (2) the root collars of individual seedlings were inconsistently located relative to groundline and soil excavation to locate and measure the groundline diameter could have led to variable impact to seedlings.

### 2.4. Canopy closure

Percent canopy closure of the overstory (and its inverse, percent open sky) was estimated by measurements from a Convex Spherical Densiometer Model-A. This was used to obtain a relative measure of light penetrating the forest overstory (Lemmon, 1956). Measurements of spherical densiometers have been found to be similar to those of hemispherical photography to predict understory light transmittance (Lhotka and Loewenstein, 2006). In August of 2007, one sample point was established at the midpoint (10 m) of each 20 m × 1 m belt transect that contained live oak seedlings. Four measurements, one in each cardinal direction, were taken per sample point, for a measure of mean percent canopy cover for each transect. The mean of the two transects per plot were used in analysis.

### 2.5. Data analysis

The data were analyzed in a randomized complete block design to test for the effect of treatment. Because of unequal numbers of sample plots among treatments, and unequal numbers of new seedlings in individual sample plots, the statistical design required unbalanced subsampling and use of the Satterthwaite method for degrees of freedom (SAS Institute, 2003). Relationships between seedling measures (height and diameter) and the variables litter depth and open sky were analyzed using correlations (CORR procedure in SAS). The MIXED procedure in SAS (SAS Institute, 2003) was used to test fixed effects of treatment, time, and the interaction of treatment and time on the response variables of seedling height and diameter, as well as percent open sky; site was considered the blocking factor. When time was included in the model, a form of repeated measures was incorporated in the analysis where the subject equaled plot. When necessary, variables were transformed using natural log or square-root transformations to satisfy the normality and homoscedasticity assumptions of the model. All plots in the experimental design ($n = 93$) were initially used in the analyses of oak seedling density in relation to oak overstory basal area. One plot was an outlier for seedling density, containing more than two times as many seedlings as any other plot; this plot was removed from our final analysis of the relationship between oak seedling density and oak basal area. Since not all plots in the experimental design had new oak seedlings present, for analyses of seedling growth parameters the experimental design included a smaller number of plots. Starting in May 2006, there were 55 plots in which chestnut oak seedlings occurred and 44 plots in which white oak occurred, with some overlap of plots in which both species occurred (Table 1). As sampling progressed and seedlings died, the number of plots used in analysis of seedling height and diameter was reduced when no seedlings were left alive in an individual plot. By August 2008, the number of plots in which live seedlings were found dropped to 40 plots for chestnut oak and 24 plots for white oak.

The effect of fire treatment and species on the binary response of mortality was analyzed for each measurement time separately in a split-plot design, using treatment as the whole-plot factor and species as the split-plot factor. Mortality was calculated cumulatively, i.e., from May 2006 to August of each year. The analysis was performed as a generalized linear mixed model with a binomial response distribution using PROC GLIMMIX in SAS. Where treatment or species-treatment interaction effects were significant, pair-wise comparisons of least squares means were performed. The influences of species and May 2006 measures of open sky, litter depth and seedling height on seedling mortality were analyzed in a logistic regression analysis using PROC LOGISTIC in SAS. For this purpose, mortality was considered cumulatively across all three growing seasons (May 2006 through August 2008), as well as on a

**Table 1**
The number of plots containing white oak (*Quercus alba*) and chestnut oak (*Q. prinus*) seedlings measured in May 2006 across treatments, and the total number of plots in each treatment for the entire study.

| | Fire-excluded | Burned 1x | Burned 3x | Total |
|---|---|---|---|---|
| *Q. alba* | 15 | 14 | 15 | 44 |
| *Q. prinus* | 21 | 22 | 12 | 55 |
| Total plots | 31 | 32 | 30 | 93 |

by-season basis, i.e., for the first (May 2006 through August 2006), the second (August 2006 through 2007), and the third growing seasons (August 2007 through 2008). Interactions of species with other variables were included in the models and were significant. As a result, logistic regression models are reported for each species separately. Variables not significant at $\alpha = 0.05$ were removed through backward elimination. The predictive ability of each model was evaluated with the *c* statistic, or concordance index, which is commonly used in logistic regression (Agresto, 2002) and for analysis of tree seedling mortality (Lhotka and Loewenstein, 2008).

## 3. Results

### 3.1. Oak seedling density

The density of chestnut oak seedlings established from acorns was relatively even across treatments, and there were no significant differences in seedling density among treatments across sampling dates ($P = 0.42$; Fig. 1). For white oaks, seedlings were less evenly distributed across treatments, yet differences among treatments were also not significant ($P = 0.23$). The number of seedlings declined significantly with year for both species ($P < .0001$ for both white oak and chestnut oak; Fig. 1). Basal area of white and chestnut oak was positively correlated with white oak and chestnut oak seedling density in May 2006 on the 1x-burn and 3x-burn treatments, but only for white oak on the fire-excluded treatment (Fig. 2). Basal area of overstory oak explained more of the variance for white oak (1x-burn $R^2 = 0.45$ ($P < 0.0001$), 3x-burn $R^2 = 0.46$ ($P < 0.0001$); control $R^2 = 0.20$ ($P = 0.0123$)) than for chestnut oak (1x-burn $R^2 = 0.15$, $P = 0.03$; 3x-burn $R^2 = 0.29$, $P = 0.0002$). Oak basal area did not explain seedling density for chestnut oak in the fire-excluded sites ($R^2 = 0.04$, $P = 0.3141$).

### 3.2. Treatment effects on litter depth and percent open sky

As expected, there were differences among treatments in the depth of litter ($P = 0.0002$) and the percent open sky ($P = 0.017$; Fig. 3). Fire-excluded sites had lower percent open sky (4.7%, SE 0.27) compared to 1x-burn sites (13%, SE 2.7; $P = 0.008$) and 3x-burn sites (12%, SE 2.4; $P = 0.02$). Percent open sky was similar between burn treatments ($P = 0.53$). Litter depth was similar between fire-excluded and 1x-burn sites (3.2 cm, SE 0.18 and 3.5 cm, SE 0.15, respectively, $P = 0.36$), whereas 3x-burn sites had significantly less litter depth (0.5 cm, SE 0.08, $P = 0.0002$ and $P = 0.0001$, fire-excluded and 1x-burn, respectively). The three treatments provided a range of litter depth and open sky conditions across the study sites (Fig. 3).

### 3.3. Seedling mortality

Seedling mortality was higher for white oak than for chestnut oak seedlings throughout the duration of the study, with final percent mortality averaging 75% for white oak compared to 55% for chestnut oak (Fig. 4). Differences in mortality among treatments were more variable. Over the first growing season, there were no differences in mortality among treatments for either species. A year later, at the end of the second growing season in August 2007, the two species responded differently. For chestnut oak, seedling mortality on fire-excluded sites was greater than on 3x-burn sites ($P = 0.0112$; Fig. 4A). For white oak, mortality of seedlings on fire-excluded sites was greater than that found on 1x-burn sites ($P = 0.0003$) and 3x-burn sites ($P = 0.0133$; Fig. 4B); mortality on burned sites was similar ($P = 0.4906$). In August 2008, there was no difference in chestnut oak mortality between fire-excluded and 1x-burn treatments, whereas for white oak there was significantly greater mortality on fire-excluded sites compared to 1x-burn ($P < 0.0001$). Observations for 3x-burn were excluded from comparisons for 2008 due to the additional burn treatment earlier that year. The greatest mortality occurred during the second growing season regardless of treatment.

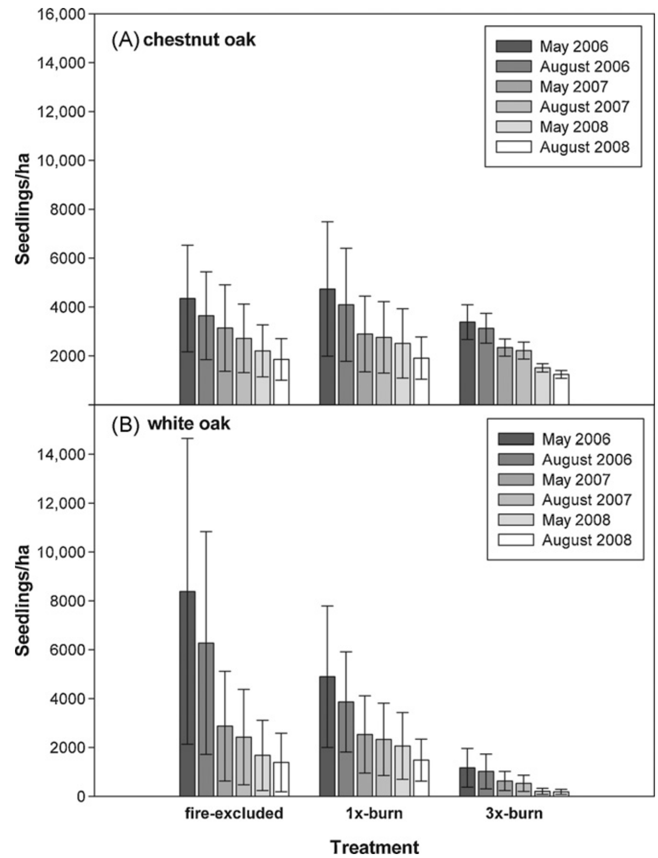


**Fig. 1.** Mean density and standard error ($n = 3$) of newly established chestnut oak (A) and white oak (B) seedlings on fire-excluded, 1x-burn and 3x-burn treatment areas measured in May and August 2006, 2007, and 2008 in the Daniel Boone National Forest, Kentucky.

Cumulative mortality of oak seedlings over the three growing seasons was significantly predicted by initial litter depth of acorns, percent open sky and initial seedling height using logistic regression (all measured in May 2006; Table 2, Fig. 5). In general, as litter depth increased so did mortality; conversely as percent open sky increased, mortality decreased. Initial seedling height, measured in May 2006, was a significant predictor of cumulative mortality, with greater height leading to higher mortality for chestnut oak, but lower mortality for white oak (Table 2). For chestnut oak, the effect of height on seedling mortality was only marginally significant ($P = 0.048$). To test whether the factors that significantly predicted oak seedling mortality differed among growing seasons, we also evaluated mortality separately for each growing season. In the first two growing seasons (May 2006–August 2006 and August 2006–August 2007) oak seedling mortality was significantly predicted by initial litter depth and percent open sky (Table 2, Fig. 5). Based on the *c* statistic values, the models had between 59% and

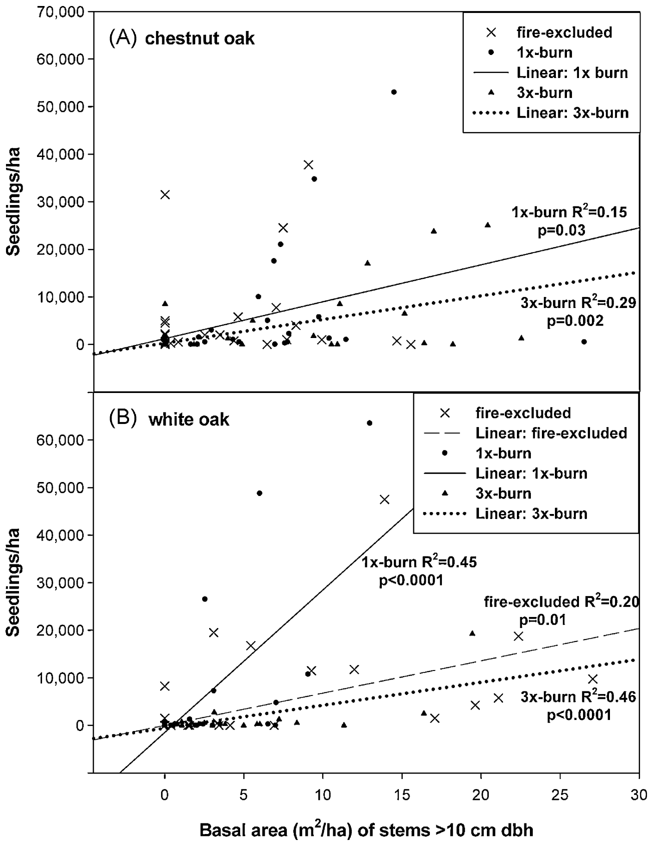


**Fig. 2.** Chestnut oak (A) and white oak (B) basal area ($m^2$/ha) and seedling density (seedlings/ha, measured in May 2006). Each point depicts the mean seedling density per plot for fire-excluded ($n = 30$), 1x-burn ($n = 32$) and 3x-burn ($n = 30$). All plots (93) in the experimental design are included, regardless of whether there were new oak seedlings present in May 2006, except for one plot in which the seedling density was two times higher than was found in any other plot.

69% probability of correctly classifying seedlings by survival and mortality ($c$ statistics ranging from 0.589 to 0.684). Again, as litter depth increased so did mortality and as percent open sky increased, mortality decreased. Initial seedling height was not a significant predictor except for white oak in the second growing season: with greater initial seedling height lower mortality was predicted (in

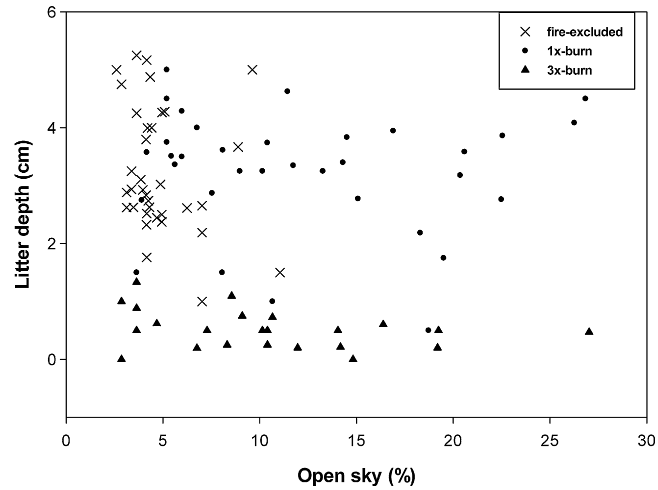


**Fig. 3.** Mean percent open sky and litter depth (cm) in May 2006 for each plot containing new oak seedlings in the Daniel Boone National Forest, Kentucky.

Fig. 5B seedling height for white oak is fixed at 9.5 cm, the median seedling height, necessary because seedling height was also significant). In the third growing season, none of the variables examined in the logistic regression analyses significantly predicted chestnut oak mortality. For white oak in the third growing season, litter depth was no longer a significant predictor of mortality, while the effect of percent open sky remained significant. Additionally, seedling height significantly predicted mortality in the third growing season for white oak; again, greater initial seedling height predicted lower mortality.

### 3.4. Seedling height and diameter

Seedling height and diameter varied by treatment and sampling period. In May 2006, seedling height differed by treatment for chestnut and white oak (Fig. 6). Chestnut oak seedlings in the 3x-burn treatment had significantly lower height compared to fire-excluded and 1x-burn treatments in the May 2006 sampling; in 2007 and 2008, there were no differences in seedling height among treatments. For white oak, seedlings in 1x-burn sites were taller than those in 3x-burn sites in 2006. In August 2007, height of white oak seedlings was higher on 1x-burn sites while seedlings

**Table 2**

Model coefficients and fit statistics for logistic regression models predicting mortality of white and chestnut oak seedlings for the duration of the study, and at the end of each growing season (August 2006, August 2007, August 2008) in the Daniel Boone National Forest, Kentucky, where $b_0$, is the intercept, $b_1$ is the coefficient for litter depth measured in May 2006, $b_2$ is the coefficient for seedling height measured in May 2006, and $b_3$ is the coefficient for percent open sky measured in mid-summer 2006.

| Mortality models | | | $b_0$ | $b_1$ | $b_2$ | $b_3$ | $c$ statistic |
|---|---|---|---|---|---|---|---|
| Cumulative Prob $CO_{Mortality\ August\ 2008}$ | = | $1/(1+\exp(-b_0 - b_1 \times \text{LitterDepth} - b_2 \times \text{HtMay06} - b_3 \times \text{OpenSky}))$ | −0.093 | 0.115** | 0.047* | −0.021** | 0.606 |
| Cumulative Prob $WO_{Mortality\ August\ 2008}$ | = | $1/(1+\exp(-b_0 - b_1 \times \text{LitterDepth} - b_2 \times \text{HtMay06} - b_3 \times \text{OpenSky}))$ | 2.118*** | 0.198*** | −0.088*** | −0.096*** | 0.663 |
| Prob May06–Aug06 $CO_{Mortality\ August\ 2006}$ | = | $1/(1+\exp(-b_0 - b_1 \times \text{LitterDepth} - b_3 \times \text{OpenSky}))$ | −2.018*** | 0.139*** | NS | −0.028** | 0.616 |
| Prob May06–Aug06 $WO_{Mortality\ August\ 2006}$ | = | $1/(1+\exp(-b_0 - b_1 \times \text{LitterDepth} - b_3 \times \text{OpenSky}))$ | −1.119*** | 0.226*** | NS | −0.136*** | 0.661 |
| Prob Aug06–Aug07 $CO_{Mortality\ August\ 2007}$ | = | $1/(1+\exp(-b_0 - b_1 \times \text{LitterDepth} - b_3 \times \text{OpenSky}))$ | −0.398** | 0.120*** | NS | −0.040*** | 0.626 |
| Prob Aug06–Aug07 $WO_{Mortality\ August\ 2007}$ | = | $1/(1+\exp(-b_0 - b_1 \times \text{LitterDepth} - b_2 \times \text{HtMay06} - b_3 \times \text{OpenSky}))$ | 1.354*** | 0.199*** | −0.077** | −0.189*** | 0.684 |
| Prob Aug07–Aug08 $CO_{Mortality\ August\ 2008}$ | = | Model not significant | | | | | |
| Prob Aug07–Aug08 $WO_{Mortality\ August\ 2008}$ | = | $1/(1+\exp(-b_0 - b_2 \times \text{HtMay06} - b_3 \times \text{OpenSky}))$ | 0.138 | NS | −0.107** | −0.060** | 0.589 |

* Significant at .05.
** Significant at .01.
*** Significant at .001.

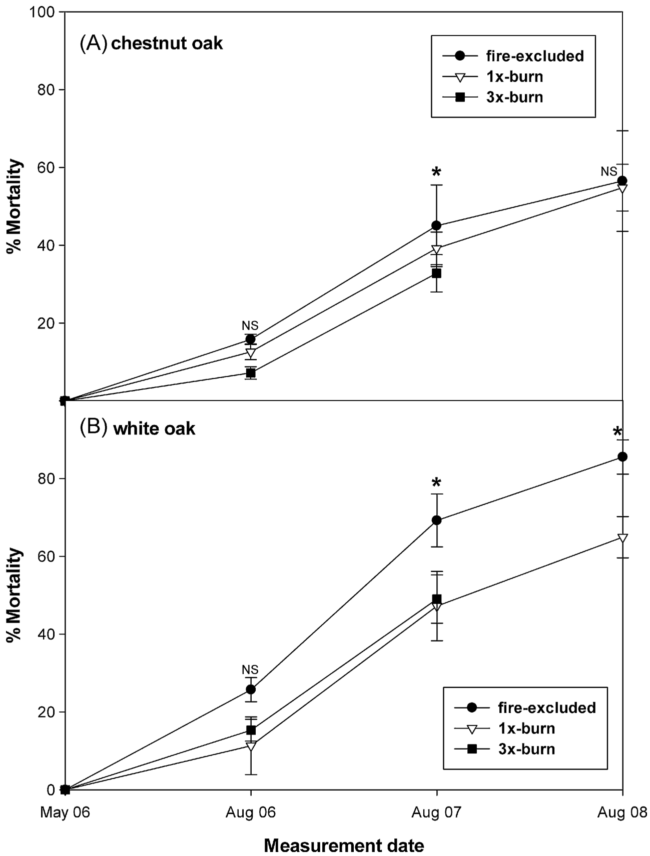


**Fig. 4.** Cumulative percent mortality for chestnut oak (A) and white oak (B) throughout the study period, based on total seedlings within each site-by-treatment combination in May 2006. For the 3x-burn sites, August 2008 mortality is omitted because these sites were burned again in April 2008, leading to substantially higher mortality than would otherwise have occurred. Error bars are standard error based on $n = 3$ study sites. Sample dates for which there was a significant effect of treatment on mortality are marked with an asterisk; dates for which no treatment differences were detected are marked 'NS'.

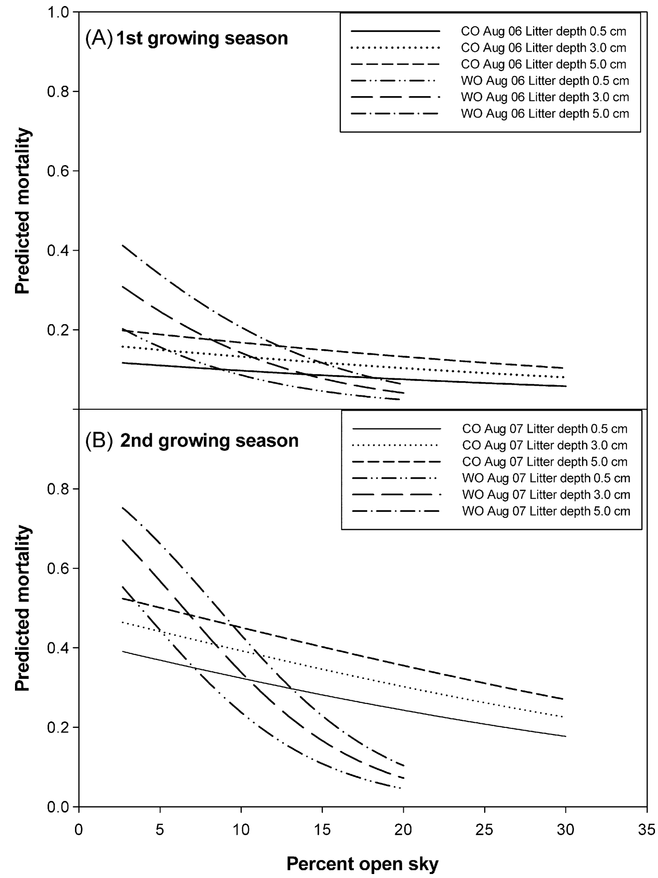


**Fig. 5.** Effect of percent open sky and litter depth on predicted mortality of chestnut oak (CO) and white oak (WO) seedlings after one growing season (A) and after the second growing season (B).

on fire-excluded and 3x-burn sites had similar mean height. In 2008, mean white oak seedling height was significantly different among all three treatments, with 3x-burn site having the smallest and 1x-burn the greatest mean seedling height. Seedling height also varied significantly among years. For chestnut oak, seedling height increased significantly with each growing season, regardless of treatment. For white oak seedlings, the growing season response was more variable among treatments. White oak seedlings in fire-excluded sites were significantly taller in 2008 compared to 2006. For 1x-burn seedlings, height increased significantly with each growing season. On 3x-burn sites, height was higher in 2007 compared to 2006, but in 2008 was similar to that measured in 2006. As a reminder, seedlings on the 3x-burn treatment were burned again in 2008. Height and diameter of seedlings surviving the 2008 burns were remeasured; the proportion of these seedlings that resprouted following fire, in 2008, was not recorded. In May 2006, seedling height was most strongly (and positively) correlated with litter depth (for chestnut oak, $R = 0.63$; $P < 0.0001$; for white oak, $R = 0.52$; $P < 0.0001$), and only weakly correlated with open sky ($R = -0.18$ for chestnut oak; $R = 0.05$ for white oak). In 2007 and 2008, the relationships between seedling height and litter depth or open sky were relatively weak and in some cases negative, ranging from $R = -0.026$ to 0.35.

Seedling diameter was measured in August 2007 and August 2008 (Fig. 7). In 2007, chestnut oak seedlings on fire-excluded sites had smaller diameter than those on both burn treatments; differences had disappeared in 2008. White oak seedlings on fire-excluded sites in 2007 had smaller diameter than those on 1x-burn sites, but similar to those on 3x-burn sites. In 2008, white oak seedlings on fire-excluded sites were similar in diameter to seedlings on both burn treatments. However, white oak seedlings on 3x-burn sites had smaller mean diameter than those on 1x-burn sites. The mean diameter in August 2007 of those seedlings that died was slightly but significantly smaller than for those seedlings that survived to August 2008 on fire-excluded sites (for chestnut oak mean diameter was 1.57 vs. 1.76, $P = 0.01$; for white oak, mean diameter was 1.21 vs. 1.36, $P = 0.02$), but not on burned sites. Seedling diameter was most strongly correlated with open sky in 2007 (for chestnut oak, $R = 0.42$; $P < 0.0001$; for white oak, $R = 0.61$; $P < 0.0001$), and less strongly correlated with open sky in 2008 (not significant for chestnut oak, $R = 0.08$; $P = 0.0555$; for white oak, $R = 0.28$; $P < 0.0001$). Correlations between seedling diameter and litter depth were generally weak, ranging from $R = -0.08$ to 0.22.

## 4. Discussion

Despite fire having been applied on the 3x-burn sites after acorns had dropped to the forest floor, chestnut oak acorn density on 3x-burn sites was similar to that on the fire-excluded and 1x-burn sites in 2006 (Fig. 1). The density of white oak seedlings appears to have been more impacted by fire, but the differences among treatments in seedling density in May 2006 were not statistically significant due to high spatial variability in seedling density across all treatments. Anecdotally, we observed that on the burned sites, some acorns were killed by burning, whereas across treatments there were many acorns that died from desiccation where

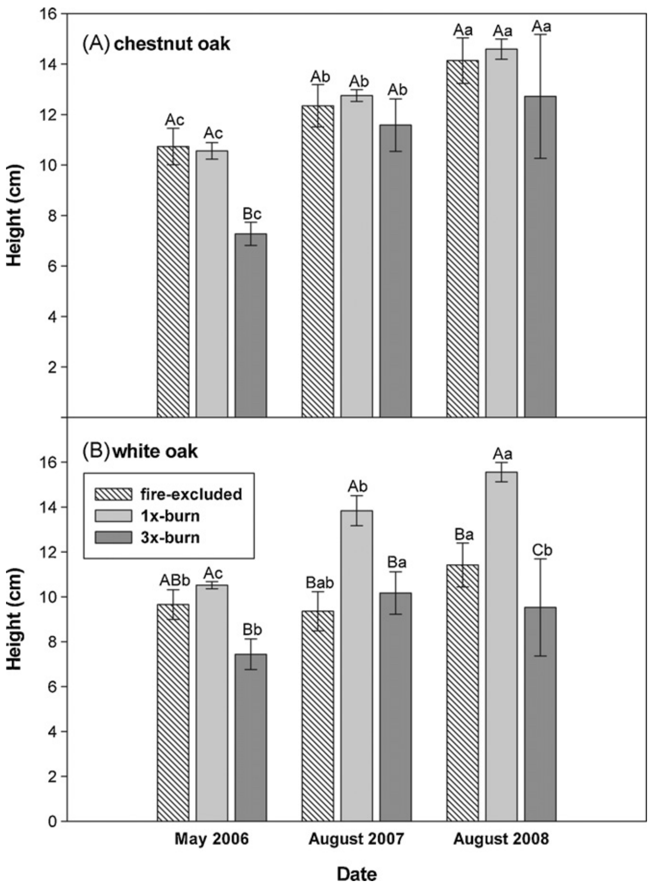


**Fig. 6.** Mean oak seedling height and standard error ($n = 3$) for chestnut oak (A) and white oak (B), measured in May 2006 and August 2007 and 2008. Different uppercase letters denote significant treatment differences within sampling period; different lower case letters denote significant differences among years for each treatment.

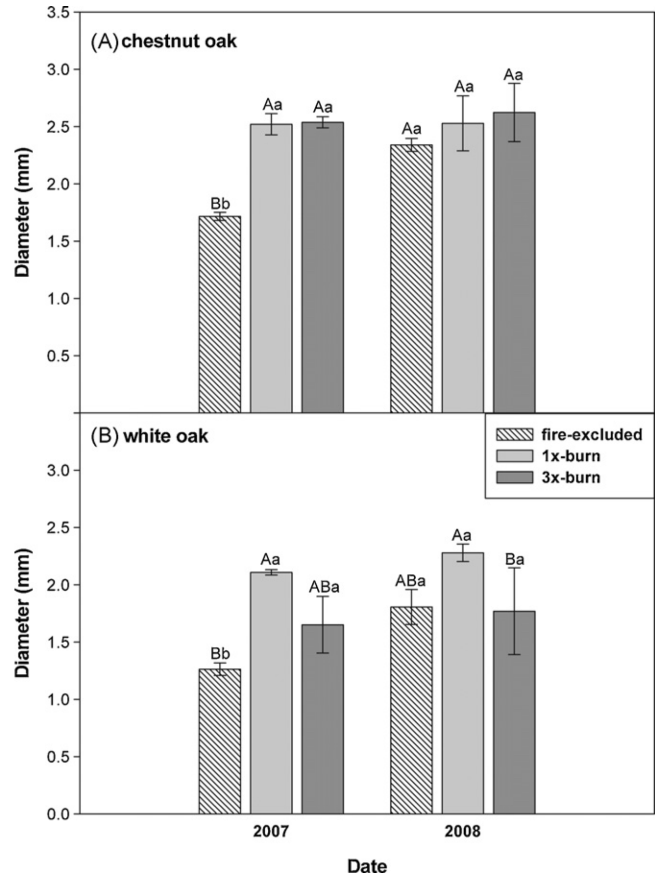


**Fig. 7.** Seedling diameter of chestnut oak (A) and white oak (B), measured in August 2007 and 2008. The mean and standard errors reported are based $n = 3$ study sites. Different uppercase letters denote significant treatment differences within sampling period; different lower case letters denote significant differences between years for each treatment.

the litter layer was thin or absent. Previous studies have shown that experimental fires can result in acorn mortality ranging from 49% (Auchmoody and Smith, 1993) to 100% (Cain and Shelton, 1998) for acorns located in the litter layer. In the latter study, acorns placed at the lower F (Oe)–mineral soil interface had much greater germinations (~90%; Cain and Shelton, 1998). Rinkes and McCarthy (2007) found that oaks and other nut species established more readily in locations with ambient amounts of litter vs. sites where litter had been experimentally removed or burned. In this study, measurements of acorn location for each seedling were taken once the seedlings had germinated and begun to establish in May 2006. Information on acorn locations at the time of prescribed fire is unknown, but it may be reasonable to assume that the great majority of acorns that gave rise to seedlings in the 3x-burn treatments were initially located in the F (Oe) horizon. Chestnut oak seeds have a thicker pericarp (i.e., acorn husk) than white oak, which may have allowed greater insulation from heating and could help to explain the similarities in chestnut oak seedling establishment across the treatments.

For both 1x- and 3x-burn treatments, and for white oak on fire-excluded sites, basal area and seedling density of each species was positively related (Fig. 2). Greenberg (2000) found that basal area of individual trees was positively related with the number of acorns/m$^2$ for white oak but not for chestnut oak. In this study we found a stronger relationship between white oak basal area and seedling density than for chestnut oak, albeit based on whole-plot measures of oak basal area, not individual tree basal area. Variable masting of overstory oaks (Greenberg, 2000) and the spatial variability of acorn predators (Rieske-Kinney, 2006) may have influenced the relationship between chestnut oak overstory basal area and acorn germination success.

White oak seedling mortality on burn treatments was lower compared to fire-excluded sites in the second and third growing seasons, whereas differences among treatments in chestnut oak seedling mortality were found only in 2007, when seedlings on fire-excluded sites had higher mortality than those on 3x-burn sites (Fig. 4). This finding is contrary to those of Wang et al. (2005) who found that fire had no effect on seedling survival after the first year. Litter depth and percent open sky were found to be significant predictors of oak seedling mortality for the duration of the study (Table 2). It should be noted that the litter depth measurement used in this analysis was made in May 2006, and therefore does not necessarily reflect the litter layer environment prior to this measurement, when acorns initially began germinating. This is an interesting and potentially confounding nuance for this study, because acorns had started germinating when the prescribed fires in the 3x-burn treatments were conducted, and it is unknown how litter cover on those sites may have influenced the establishment of individual seedlings. For example, loose litter covering acorns over winter helps to protect acorns against desiccation (Barrett, 1931). Sites burned in 2006, after acorns had overwintered, would have had less litter at the time of measurement than they had during the winter period. Thus, the litter depth measurement may not accurately reflect the positive effects of somewhat greater amounts of fresh litter during the winter. Conversely, while wintertime litter protection may help to explain the trend towards higher density of new white oak seedlings in the fire-excluded sites compared to the 1x- and 3x-burn sites, once seedlings established, greater litter depth combined with nearly closed canopies led to the higher seedling mortality in fire-excluded sites compared to burned sites. This suggests that seedlings developing in thick litter layers may deplete acorn cotyledon energy reserves faster than seedlings developing in minimal litter, leading to potentially higher mortality rates. Greater seedling height was correlated with deeper litter, especially in the first year (2006), and this is likely due to the greater stem elongation required to emerge from deeper litter, and not necessarily a measure of future seedling fitness.

White and chestnut oak seedlings in the 1x-burn treatments and chestnut oak seedlings in the 3x-burn treatments had greater basal diameters than those in fire-excluded sites in 2007. This could be attributed to greater light availability measured as percent open sky (Fig. 3). These results are corroborated by findings from Wang et al. (2005) who found that biomass of white oak seedlings established from seed in recently burned stands was greater than the biomass of new seedlings in fire-excluded stands. However, in 2008, differences in seedling diameter among treatments had mostly disappeared, in part because the seedlings that died on the fire-excluded sites had significantly smaller diameters and possibly lower carbon reserves and thus less growth potential. However, the differences in mean diameter between those seedlings that died and those that survived to 2008 were small, suggesting that other factors may also have contributed to the disappearance of diameter differences between seedlings on fire-excluded sites and burned sites.

Prior research on these and similar sites has demonstrated that low intensity prescribed fire may not be effective in increasing the competitiveness of oak advance reproduction compared to competitors such as red maple (Alexander et al., 2008; Green et al., 2010). However, if fire is applied at the appropriate time, oak regeneration from new acorns may benefit. Stringer and Taylor (1999) found greater germination success in sites treated with experimental fires prior to acorns being placed on the ground compared to untreated sites, and this study suggests a potential growth advantage to seedlings that establish after fire, when litter has been reduced and light availability increased. Thus, if a stand is deemed to be poorly stocked with advance regeneration, visual surveys of acorn production may be used to identify an impending mast crop, and a prescribed fire could be implemented (prior to dispersal in late summer or early fall) to create a more desirable seedbed for acorn germination; this may be especially beneficial for the white oak group for which radicles emerge in the autumn. In this context, prescribed fires conducted in late summer or early fall would be preferable, thereby reducing the litter layer prior to acorn drop, as well as before autumn leaf fall, when fresh litter could potentially afford acorns adequate protection from desiccation over winter. In addition, after germination in the spring, the developing seedlings could potentially become more competitive in the presence of increased light. Prescribed fire in this region is rarely conducted at this time of year, although it is possible (Brose and VanLear, 1998); research examining the potential for this shift in timing should consider the impacts to new oak seedlings following significant acorn crops.

## 5. Conclusions

Much of the literature on the effects of prescribed fire on oak regeneration focuses on the oak advance regeneration pool, targeting responses of oaks and their competitor species by examining changes in stem density with treatment (Albrecht and McCarthy, 2006; Brose et al., 1999; Iverson et al., 2008), or seedling population studies wherein marked seedlings or advance regeneration are followed through time in response to treatments (Alexander et al., 2008; Dey and Hartman, 2005; Green et al., 2010). There are few studies that examine the responses of new seedlings to fire, likely because of the difficulty in timing prescribed fire treatments to coincide with oak mast events, yet this may be an important aspect for future management to improve oak regeneration. The occurrence of an oak mast event on our study sites in 2005 was serendipitously timed to allow us to examine oak seedling establishment, survival and growth in the context of prior burning, which created variability in litter depth and light availability. We found that white oak seedlings originating from seed and establishing in burn treatments displayed more vigorous growth, on average, than seedlings establishing in fire-excluded treatments in the first two growing seasons; this was less true for chestnut oak. In addition, seedling survival in burn treatments was greater than in the relatively closed canopy of the fire-excluded treatments, especially for white oak. Prescribed fires result in significant topkill and mortality of small to medium-sized trees (Blankenship and Arthur, 2006; Green, 2005), and consume a significant portion of the leaf litter layer (Loucks et al., 2008). Both of these effects had positive feedbacks for oak seedlings establishing and developing in recently burned stands. Evidence from this study and our prior research (Alexander et al., 2008; Green et al., 2010) suggests that oak seedlings established and growing on recently burned sites may be more competitive than oak seedlings that have developed and persisted under nearly closed-canopy stands, if and when a future full or partial overstory release occurs. However, differences in the responses of white and chestnut oak merit consideration of the importance and timing of reductions in the litter layer, and it is likely that a broader suite of oak species in our study would have yielded even more varied responses than found for these two species.

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