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Survival and growth of upland oak and co-occurring competitor seedlings following single and repeated prescribed fires

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ABSTRACT

Studies within and outside the U.S. indicate recurring oak (*Quercus* spp.) regeneration problems. In deciduous forests of the eastern U.S., a prevailing explanation for this trend is fire suppression leading to high competitor abundance and low understory light. In response, prescribed fire is increasingly used as a management tool to remedy these conditions and encourage future oak establishment and growth. Within eastern Kentucky, we implemented single and repeated (3×) prescribed fires over a 6-yr period (2002–2007). Pre- and post-burn, we quantified canopy cover and oak seedling survival and growth compared to other woody seedlings deemed potential competitors, primarily red maple (*Acer rubrum* L.) and sassafras (*Sassafras albidum* (Nutt.) Nees.). Burning temporarily decreased canopy cover 3–10%, but cover rebounded the subsequent growing season. Repeated burning ultimately produced canopy cover about 6% lower than sites unburned and burned once, suggesting a cumulative effect on understory light.

Oak regeneration

Red maple exhibited low survival (~40%) following single and repeated burns, but growth remained similar to unburned seedlings. Burning had little impact on sassafras survival and led to total height and basal diameters 2× greater than unburned seedlings. A single burn had no impact on red oak (*Erythrobalanus* spp.) survival and increased height and basal diameters 25–30%, but this positive growth response was driven by seedlings on several plots which experienced high burn temperatures and consequently high overstory mortality. White oaks (*Leucobalanus* spp.), however, exhibited twice as high mortality compared to those unburned, with no change in growth parameters. Repeated burning negatively impacted survival and growth of both oak groups compared to unburned seedlings. With both burn regimes, oaks with smaller pre-burn basal diameters exhibited the lowest post-burn survival. Thus, despite the ability of prescribed burns to temporarily increase understory light and reduce red maple survival, neither single or repeated burns placed oaks in an improved competitive position. These findings result from a combination of highly variable yet interdependent factors including the (1) life history traits of oaks compared to their co-occurring competitors, (2) pre-burn stature of pre-existing oak seedlings, and (3) variability in fire temperature and effects on understory light.

1. Introduction

Oaks (*Quercus* spp.) comprise a large, diverse genus of ~400 species worldwide distributed across various biomes, including temperate deciduous forests, chaparrals, savannahs, and broad-leaf evergreen forests (Johnson et al., 2002). This genus is important not only in terms of dominance, but also in its production of a nutrient-rich, hard mast consumed by numerous birds and mammals (McShea and Healy, 2002). Oaks have been deemed keystone species because of their cascading effects on wildlife species (Fralish, 2004) and foundation species because of their direct and indirect influences on overall community dynamics and ecosystem processes (Ellison et al., 2005; McShea et al., 2007).

Studies both within and outside the U.S. indicate recurring problems with oak regeneration, a complex, lengthy process consisting of flowering and pollination, acorn production, acorn germination and seedling establishment, seedling development, and eventual overstory recruitment following canopy release. Impediments to oak regeneration may arise naturally from

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weather, pests, and pathogens (Johnson et al., 2002), but studies often reveal problems in forests with considerable human influence. For instance, altered disturbance regimes in Scotland have decreased understory light and increased competition (Humphrey and Swaine, 1997). Habitat fragmentation and heavy urbanization have promoted large rodent populations in China, increasing acorn predation (Sun et al., 2004), and diseases and stress in Italy have increased overstory mortality leading to reduced acorn abundance (Vettraino et al., 2002).

In deciduous forests of the eastern U.S., a prevailing explanation for poor oak regeneration is fire suppression and consequently high competitor abundance and low understory light (Abrams, 1992; Abrams and Nowacki, 1992). Pollen records demonstrate decreased oak pollen and increased pollen of fire-sensitive species since initiation of fire suppression ~1930 (Delcourt and Delcourt, 1997), and dendrochronological analyses of fire scars show widespread, frequent fires during or just prior to the establishment of current oak overstories (McEwan et al., 2007). Paradoxically, recent modeling of climate change impacts to species in eastern U.S. forests suggest upland oak populations should increase as conditions become hotter and drier, while fire-sensitive species like red maple (*Acer rubrum* L.) should decrease (Iverson and Prasad, 2002).

Ecologically, upland oaks have life history traits suggesting they are fire-adapted. Their conservative growth strategy promotes a large root system, which facilitates resprouting after top-kill and efficient water and nutrient use (Lorimer, 1985; Abrams, 1992) in dry, fire-prone habitats. Most oaks have moderate shade-tolerance (Burns and Honkala, 1990) and are successful in relatively high light environments where low moisture is a key limiting factor to competitors (Abrams, 1992). In contrast, many fire-sensitive species thrive in the absence of fire disturbances because of their

Climate is humid, temperate, and continental with hot summers and mild winters. Annual air temperature averages 12.8 °C, with mean daily temperatures of 0.5 °C in January and 24 °C in July. Mean annual precipitation (122 cm) is equally distributed throughout the year (Foster and Conner, 2001).

Forest stands were second-growth, about 80 yr old, and ranged in oak site index from SI 50 to 100. Pre-burn basal area of stems ≥10 cm diameter at breast height (DBH) averaged 20–30 m^2 ha^{-1}, and oak and hickory (*Carya* spp.) dominated the overstory. Prevalent overstory red oaks (*Erythrobalanus* spp.) on mid- and upper slopes included scarlet (*Q. coccinea* Muenchh) and black (*Q. velutina* Lam.) oak, with northern red oak (*Q. rubra* L.) common on lower slopes. Prevalent white oak species (*Leucobalanus* spp.) were white (*Q. alba* L.) and chestnut oak (*Q. montana* L.). Maples (*Acer* spp.), downy serviceberry (*Amelanchier arborea* (Michx. f.) Fern), black gum (*Nyssa sylvatica* Marshall), and sourwood (*Oxydendrum arboreum* (L.) DC.) dominated the midstory (2–10 cm DBH). Red maple comprised ~45% of midstory stem density, while oaks comprised <3%.

2.2. Experimental design

Within an 18-km^2 area, three study sites (Buck Creek, Chestnut Cliffs, and Wolf Pen) of ~200 to 300 ha each were subdivided into three burn treatments encompassing 58–116 ha. Treatments were an unburned control, less frequently burned (5+ yr interval), and frequently burned (1–2 yr interval), and were selected based on prior studies suggesting a <5-yr burn interval to suppress growth of woody competitors, such as red maple (Sander, 1988), and historical evidence that low-intensity surface fires occurred in the region every 3–4 yr (Sutherland, 1997).

Within each treatment, 8–12 sample plots were chosen using a higher shade tolerance and non-conservative growth strategy, which allow greater height growth than oaks under a dense canopy (Lorimer et al., 1994). Without disturbances to decrease cover of these shade-tolerant species, they can reduce understory light, further impeding oak development (Loftis, 1990b; Lorimer et al., 1994). Smaller oak seedlings are often less successful following release (Loftis, 1990a), primarily because they are unable to compete with faster-growing, shade-intolerant species of seed origin like yellow-poplar (*Liriodendron tulipifera* L.) and sprouts of residual stems of shade-tolerant species (Beck and Hooper, 1986).

In theory, prescribed fires could enhance oak regeneration by increasing understory light and decreasing competition from co-occurring, fire-sensitive species, thereby providing a population of oak seedlings of sufficient size to compete following a disturbance-generated canopy opening. Fire could also provide a canopy release if post-fire mortality of overstory trees was substantial. To understand the ability of prescribed fire to create these conditions, we quantified pre- and post-burn canopy cover and individual oak seedling growth and survival compared to other woody seedlings deemed potential competitors, primarily red maple and sassafras (*Sassafras albidum* (Nutt.) Nees.). These species differ from oaks and each other in their life history traits, namely shade tolerance and growth strategies. This study capitalizes on sites encompassing a diverse terrain, a large number (~3000) of pre-established woody seedlings, a relatively long-term data set (6-yr), and both single and multiple (3×s) burns.

2. Methods

2.1. Study area

This study was conducted in the Cumberland Ranger District of the Daniel Boone National Forest (DBNF) of eastern Kentucky.

grid overlaid on a topographic map. Plots were 10-m wide × 40-m long and arrayed parallel to topographic contours. Plots encompassed a variety of aspects, slopes (often exceeding 60%), and elevation (260–360 m) and were classified as sub-xeric, intermediate, or sub-mesic (McNab et al., 2007) to objectively account for this variability, which could affect fire behavior (Loucks et al., 2008).

2.3. Prescribed fires

The U.S. Forest Service conducted fires using drip torches and helicopter ignition. Frequently burned sites were burned spring 2003, 2004, and 2006, while infrequently burned sites were burned spring 2003; future references to treatments will be "Burned 1×" and "Burned 3×." All burns were conducted between March 26 and April 16, when air temperatures were 20–27 °C, and relative humidity was 23–45% (Table 1). Late spring burns were used to maximize impacts on competitors during bud swell, a period when seedlings have reduced root carbohydrate reserves. The large size and highly dissected topography of our study sites and concern for personnel safety prevented assessment of flame height and spread rates (*i.e.*, fire intensity); thus, fire temperatures were recorded at four locations within each plot via pyrometers (Loucks et al., 2008). Because of the relatively steep slopes present across our plots and fuel discontinuity after the previous year's burn, several plots within Wolf Pen and Buck Creek did not burn during the 2004 fire, leading to relatively low burn temperatures.

2.4. Canopy cover

Canopy cover was estimated using hemispherical photography at three locations (10, 20, and 30 m) along the bottom axis of each sampling plot within the Buck Creek study site only, due to

Table 1
Burn parameters within the three study sites averaged throughout each fire's duration

Burn parameters	Buck Creek				Chestnut Cliffs				Wolf Pen			
	Burned 1×	Burned 3×			Burned 1×	Burned 3×			Burned 1×	Burned 3×		
Date	4/14/03	4/14/03	3/26/04	4/11/06	3/25/03	3/24/03	4/7/04	4/13/06	4/16/03	4/16/03	4/7/04	4/11/06
Time of ignition	1130	1130	1300	1015	1130	1230	1200	1130	1230	1230	1200	1000
Ignition method	Aerial	Aerial	Hand	Hand	Hand	Hand	Aerial	Hand	Aerial	Aerial	Aerial	Hand
Air temperature (°C)	26.3	26.3	25.2	24.1	25.0	24.0	23.4	25.4	26.8	26.8	23.1	20.0
Relative humidity (%)	23.2	23.2	44.6	28.0	32.5	35.0	39.7	35.0	38.7	38.7	39.0	30.5
Wind direction	NW	NW	SW	SW	SW	W	W	S	W	W	W	W
Wind speed (km/h)	0–9.7	0–9.7	3.2–9.7	1.6–3.2	0–9.7	0–9	3.2–6.4	4.8–7.6	0–14.48	0–14.48	8–12.9	3.2–6.4
Mean burn temperature @ 0 cm (°C)	473.2	563.7	148.5	529.0	533.1	475.0	410.5	485.1	583.5	561.3	152.3	476.0

sampling logistics. Photographs were taken either before dawn, after dusk, or when overcast to limit uneven exposure due to direct sunlight. In 2005, measurements were only taken at the 10-m location. Photographs were taken 80 cm above the forest floor using a Nikon FC-E8 183° fisheye converter attached to a digital camera, placed on a Delta-T Devices self-leveling mount, and positioned toward magnetic N. Prior to image analysis using HemiView 2.1, Adobe Photoshop® was used to remove lighted direction markers and help maximize contrast between open sky and canopy. Images were analyzed at random and evaluated three times by a single analyst to produce an average canopy cover value for each location at each plot.

2.5. Seedling survival and growth

To determine seedling survival and growth, ~3000 seedlings of oaks and their most predominant competitors were permanently tagged in June 2002 prior to burning. We selected any available seedling from the pool of advance regeneration (98% of selected

measurements of basal diameter were made with a digital caliper where the stem exited the soil. Total height was measured with a ruler from stem base to the leading shoot tip, and annual height growth was measured on the leading shoot from the last visible bud scar to the shoot tip. Seedlings were considered dead when no trace of shoot or root, or live tissues, were found. Seedlings recorded dead the previous year but that had re-sprouted the next were re-classified as alive for the prior sampling period. Seedlings not located were removed from subsequent analyses. According to our pyrometer data, the 2003 and 2006 fires burned every plot, and 93 and 95%, respectively, of the seedlings in the population study which were still alive after these fires had been top-killed. The 2004 burn was patchy because of discontinuous fuels (Loucks et al., 2008). Ten plots did not burn, and portions of many other plots were unburned. Consequently, only 44% of seedlings still alive after burning in 2004 had been top-killed.

2.6. Statistics

seedling from the pool of advance regeneration (98% of selected seedlings were ≤60 cm; mean height of 21.5 ± 14.1 cm; bud scars visible from multiple years), and did not observe or mark any true seedlings. To facilitate re-measurement, seedlings were tagged with a unique identification number and mapped. Seedlings typically included 10 individuals each of the dominant white (*Leucobalanus* spp.) and red oak (*Erythrobalanus* spp.) subgenera and the most abundant competitor species, totaling ~30 individual seedlings per plot. On occasion, only a single oak species was present, or multiple species within subgenera were needed to obtain 10 oak seedlings. Plots encompassed a variety of species assemblages distributed across landscape positions (Table 2).

Annually, from 2002 to 2007, seedlings were measured during the growing season (June–August) for survival, basal diameter, total stem height, and annual height growth. Two perpendicular

For each seedling group, annual seedling survival (%) was computed across all plots within each site × treatment combination. These data were arcsine transformed to achieve a normal distribution, and analyzed as a split-plot fixed effects model with treatment blocked within study site using PROC MIXED (SAS Institute 2000). Mean basal diameter and total height were calculated for each seedling group within each plot, and analyzed similarly for temporal and treatment effects, but using plot as a repeated measure. Hemispherical photographs, acquired only within Buck Creek, generated a pseudoreplicated design for canopy cover analysis. Plot was used as the experimental unit. Response variables were also analyzed for differences among landscape positions; however, not all treatments within each site contained every landscape position (see Table 2). Thus, landscape

Table 2
Number of plots containing each measured seedling species across sub-mesic (sm), intermediate (int), and sub-xeric (sx) landscape positions

Group	Species	Unburned			Burned 1×			Burned 3×			Total
		sm	int	sx	sm	int	sx	sm	int	sx	
Red oaks	Black oak (*Quercus velutina*)	14	5	4	5	14	7	6	15	4	74
	Northern red oak (*Quercus rubra*)	13	–	–	4	3	3	6	2	–	31
	Scarlet oak (*Quercus coccinea*)	–	3	3	1	2	2	1	4	4	20
White oaks	White oak (*Quercus alba*)	15	5	2	4	8	3	7	6	3	53
	Chestnut oak (*Quercus montana*)	6	6	2	3	8	5	1	11	3	45
	Chinkapin oak (*Quercus muehlenbergii*)	–	–	–	–	–	–	2	–	–	2
Others	Sassafras (*Sassafras albidum*)	1	3	3	3	6	7	–	7	5	35
	Red maple (*Acer rubrum*)	4	4	1	1	8	2	–	6	1	27
	White ash (*Fraxinus americana*)	8	–	–	1	–	–	3	2	–	14
	Sugar maple (*Acer saccharum*)	3	1	–	1	1	–	5	–	–	11
	Hickory (*Carya* spp.)	1	1	–	–	1	–	–	–	–	3
	Eastern redbud (*Cercis canadensis*)	–	–	–	–	–	–	–	1	–	1

effects were analyzed across treatments, without blocking for site. Analysis at the landscape level produced few significant results. Therefore we only present data for the overall analyses without landscape position but briefly describe the effects of landscape position on survival data, which was the only response variable with a significant effect of landscape position. Site and the site × treatment interaction were considered random effects in the model when analyzed without landscape position. Fixed effects were treatment, year, seedling group, and landscape position when analyzed, and their interactions. For all analyses, Type III tests of fixed effects were used to assess significant factors and interactions ($P < 0.05$), and because the design was unbalanced, we used a Satterthwaite method to estimate degrees of freedom. For significant effects, least square means were compared via a post hoc Fischer's LSD test to determine differences among means at an alpha level of 0.05.

Because the same oak species did not occur across all plots, seedlings were pooled into red oak or white oak subgenera. Comparisons were made between oak subgenera, red maple, and sassafras. We chose to analyze these competitor species because of their dominance across treatments and landscape positions and because analyses of other competitors indicated that white ash (*Fraxinus americana* L.) and eastern redbud (*Cercis canadensis* L.) behaved similarly to red maple, while hickories behaved similarly to white oaks. Sugar maple (*Acer saccharum* Marshall) exhibited a distinct trend (extremely high post-burn mortality and slow growth), but this species was primarily limited to submesic plots.

Percent survival across all sites within each burn treatment based on initial basal diameter was calculated for each seedling group by grouping individual seedlings by initial diameter size classes (≤ 2.0, 2.1–3.0, 3.1–4.0, 4.1–5.0, and >5.0 mm) and tallying

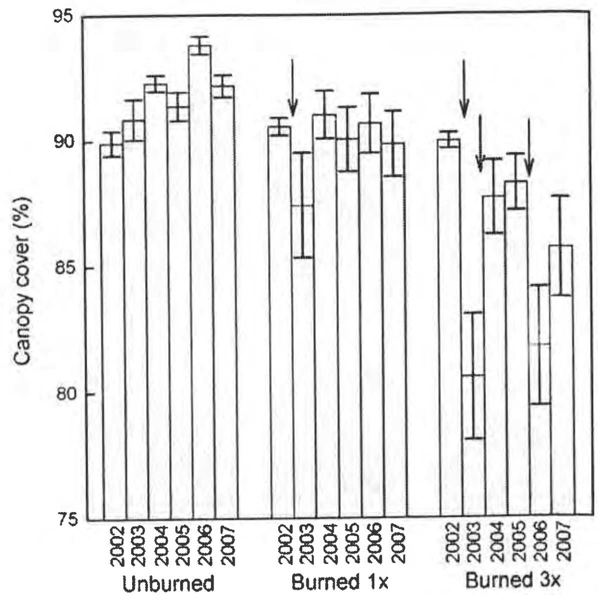


Fig. 1. Annual canopy cover within each burn treatment at Buck Creek study site. Mean data ± S.E. Arrows indicate burn.

pre-burn ($P < 0.01$) and 5 and 7% lower than sites unburned ($P < 0.01$) and burned 1× ($P = 0.03$), respectively.

3.2. Seedling survival

There was a significant three-way interaction of treatment, survival in subsequent years. To determine if there were significant ($\alpha = 0.05$) linear relationships between seedling basal diameter and total height, 2007 annual height growth and previous year canopy cover, and burn temperature and seedling survival, we utilized the REG procedure within SAS. For each relationship, we report the P-value for the ANOVA results of the overall model and/or the coefficient of determination (R^2) to describe the strength of the relationship. For the linear regressions of basal diameter and total height, we report the equation for the regression model for each seedling group and treatment ($y = mx + b$, where the regression coefficients m = slope and b = y-intercept). In fall 2006, five Wolf Pen control plots were burned accidentally, and data from these plots were omitted from 2007 analyses.

3. Results

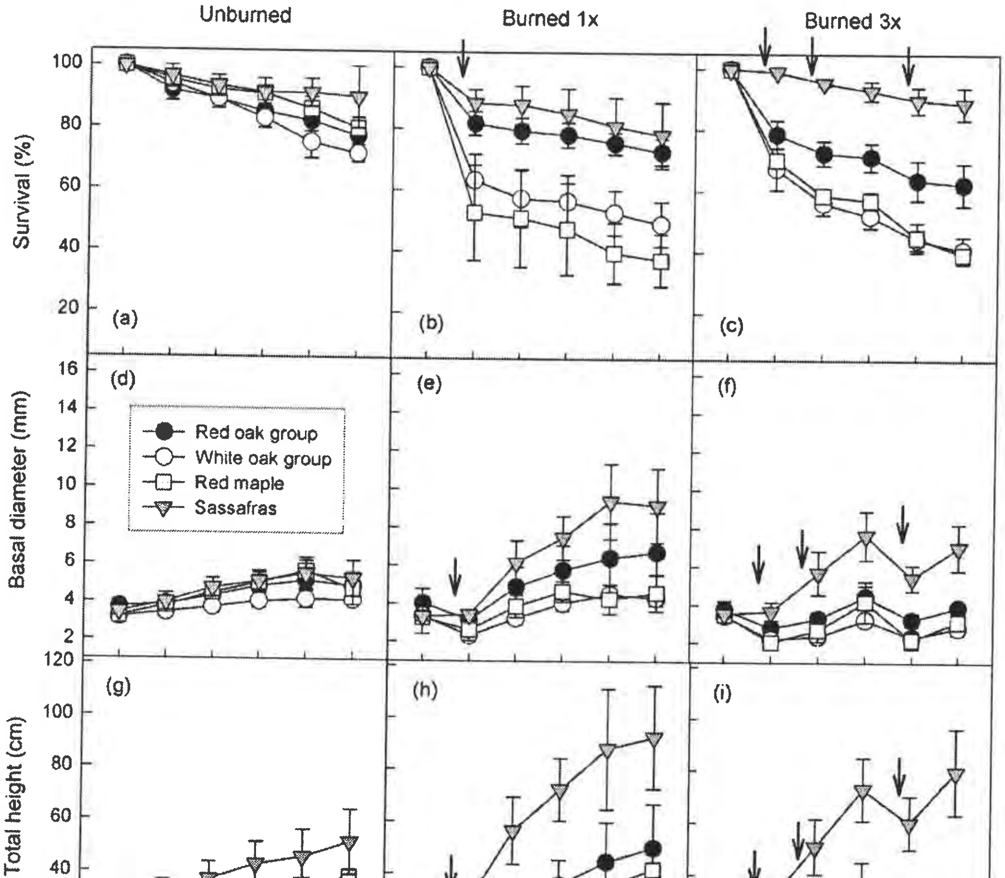
3.1. Canopy cover

There was a significant interaction between treatment and sampling year on canopy cover ($P < 0.001$) with no effect of landscape position ($P = 0.26$). On unburned sites, cover varied between 90 and 94% (Fig. 1). Cover temporarily decreased ~3% ($P = 0.02$) on sites burned 1×, but values the subsequent growing season were similar to those pre-burn ($P = 0.73$). On sites burned repeatedly, the initial burn reduced cover 10% ($P < 0.01$), three times more than sites burned once ($P < 0.01$), indicating that even fires conducted at similar times can produce variable outcomes. Canopy cover rebounded the next summer, and was only 2% less than pre-burn ($P = 0.08$) despite being burned a second time 3 mo prior, likely reflecting relatively mild burn temperatures (see Table 1). The third burn reduced canopy cover ~6% from the previous year ($P < 0.01$). Although cover recovered about 2% by 2007, repeatedly burned sites still had cover 5% lower than

seedling group, and landscape position on seedling survival ($P < 0.001$), but there was no relationship between burn temperature and seedling survival for any seedling group or burn ($P > 0.05$ for all). There was also a significant effect of year that was independent of other main factors ($P < 0.01$) because earlier sampling years always had higher survival than later years. In the absence of fire, white oaks declined ~6% annually, compared to about 5% for red oaks and red maple (Fig. 2a). These three seedling groups exhibited the highest mortality on sub-mesic sites. Sassafras survival remained >90% throughout study duration. This species' mortality was greatest on intermediate sites where survival was only ~70% in 2007, but sassafras exhibited no mortality on sub-mesic sites. Red maples tended to have significantly higher survival than red oaks and sassafras on sub-xeric sites ($P = 0.05$ and 0.02, respectively) and higher survival than sassafras, white oaks, and red oaks ($P < 0.01$, 0.02, and 0.01, respectively) on intermediate sites. Thus, under all moisture regimes, at least one competitor performed equivalent to or better than co-occurring oaks.

Burning 1× decreased red maple and white oak survival to 50% ($P < 0.01$) and 60% ($P = 0.06$), respectively, but survival of sassafras and red oaks remained similar to unburned controls (Fig. 2b; $P = 0.10$ and 0.08, respectively). Low red maple survival was due to initially high post-burn mortality on sub-xeric and intermediate sites and delayed mortality on sub-mesic sites. White oak mortality was consistently high across all landscape positions.

Sites burned 3× had lower white oak and red maple survival compared to unburned sites ($P = 0.04$ and <0.01, respectively), but sassafras and red oaks were not significantly affected (Fig. 2c; $P = 0.88$ and 0.30, respectively). Importantly, survival of all groups was no different than those burned only 1× ($P = 0.54$, 0.36, 0.27, and 0.89 for white oaks, red oaks, sassafras, and red maple, respectively). Across landscape positions, seedling survival generally mimicked overall trends except oaks on sub-mesic sites had


Unburned
Burned 1x
Burned 3x
Survival (%)
100
80
60
40
20
(a)
(b)
(c)
Basal diameter (mm)
16
14
12
10
8
6
4
2
(d)
(e)
(f)
Red oak group
White oak group
Red maple
Sassafras
Total height (cm)
120
100
80
60
40
(g)
(h)
(i)

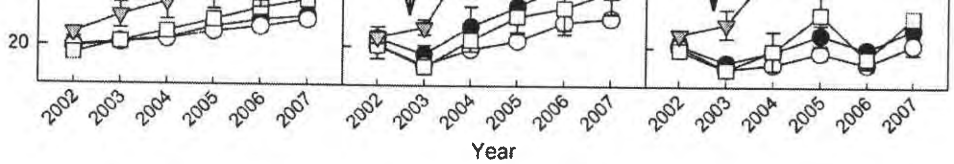


Fig. 2. Annual survival, basal diameter, and total height (mean ± S.E.) for each seedling group within each burn treatment. Arrows indicate burns.

survival significantly lower than those on sub-xeric and intermediate sites burned 3× ($P < 0.01$ for all) and lower than unburned sub-mesic sites ($P < 0.01$ for all).

3.3. *Basal diameter*

The effect of burn treatment on seedling basal diameter depended on its interaction with seedling group and sampling year (treatment × seedling group × year, $P < 0.001$), and was independent of landscape position ($P = 0.35$). On unburned sites, mean basal diameter of all seedling groups slowly increased over the 6-yr study (Fig. 2d). Red oaks and red maple increased from ~3.5 to 5.0 mm ($P < 0.01$ for both). White oaks grew more slowly, but increased from 3.2 to 4.1 mm ($P = 0.04$). Sassafras increased from 3.5 to 5.2 mm, but this effect was not significant ($P = 0.14$).

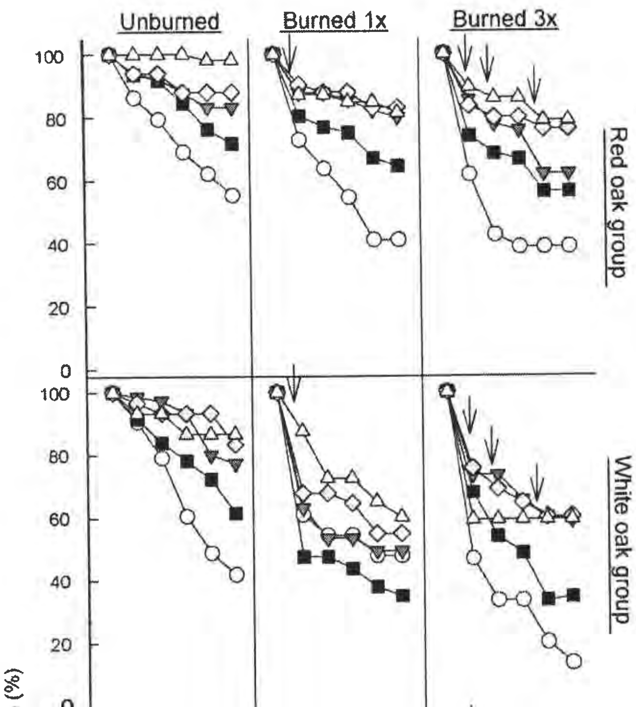
On sites burned 1×, red oaks and sassafras exhibited large increases in mean diameter from 2002 to 2007 ($P < 0.01$ for both), such that by 2007, red oaks had diameters 2 mm larger than those unburned ($P = 0.02$), while sassafras diameters were 4 mm larger ($P < 0.01$; Fig. 2e). White oak and red maple seedlings slightly increased over time but remained similar to unburned controls by 2007 ($P = 0.65$ and 0.72, respectively) and about 2× smaller than sassafras and 1.5× smaller than red oaks.

Multiple burns periodically reduced diameters of all seedling groups, due to top-kill and re-sprouting of new stems with smaller diameters (Fig. 2f), although the 2004 burn had minimal impacts, likely due to relatively low burn temperatures. By 2007, no seedling group had diameters greater than those on unburned sites ($P = 0.28$, 0.65, 0.06, and 0.20 for red oaks, white oaks, sassafras, and red maple, respectively), and diameters of red oaks and sassafras were smaller than those on sites burned 1× ($P < 0.01$ for both).

Across treatments and seedling groups, seedlings with larger initial basal diameters generally had the greatest survival over the study (Fig. 3). On unburned sites, there were linear decreases in red and white oak survival across diameter size classes, but the slope of these lines tended to increase with decreasing size. Unburned red maple <2 mm also exhibited a linear decrease in survival with basal diameter, but larger size classes tended to have reduced survival only in later study years. Burning also produced the lowest survival among smaller size classes, but trends were generally curvilinear, with most mortality occurring after the initial burn. Notably, single and repeated burns produced especially low survival of small red maple (<2 mm), and small white oaks (<3 mm) were most impacted by multiple burns. Except for a linear decrease in small sassafras burned 1×, this seedling group exhibited few survival trends as a function of size class.

3.4. Total height

The effect of burn treatment on seedling total height depended on its interaction with seedling group and sampling year



(treatment × seedling group × year; $P < 0.001$), and was independent of landscape position ($P = 0.86$). On unburned sites, mean height of all seedling groups slowly increased from 2002 to 2007 (Fig. 2g). Sassafras seedlings doubled in height from ~25 to 50 cm ($P < 0.01$), as did red maple, which increased from ~17 to 34 cm ($P < 0.01$). Both red oaks and white oaks grew ~2 cm annually, increasing significantly ($P < 0.01$ for both) in height from about 20 to 30 cm over the 6-yr period.

By 2007, sassafras and red oak seedlings burned 1× were 41 and 11 cm taller, respectively, than those unburned ($P < 0.01$ for both), but red maple and white oaks were no taller than unburned seedlings ($P = 0.72$ and 0.82, respectively; Fig. 2h). Sassafras quadrupled in height from 2002 to 2007 (from 23.7 to 83.2 cm; $P < 0.01$), and red oaks grew from 23.2 to 50.2 cm tall ($P < 0.01$). This large increase in red oak height (and basal diameter) was mostly on several Wolf Pen plots burned 1×, which had higher burn temperatures compared to nearby plots and consequently high reductions in overstory basal area (Fig. 4).

Sassafras and red oaks burned 3× were taller in 2007 than they were in 2002 ($P < 0.01$ and 0.02, respectively), but white oaks ($P = 0.93$) and red maple ($P = 0.08$) had heights similar to those pre-burn (Fig. 2i). Compared to unburned seedlings, sassafras burned 3× were 28 cm taller by 2007 ($P < 0.01$), but red oaks, white oaks, and red maple remained similar to unburned controls ($P = 0.65$, 0.26, and 0.25, respectively). Sassafras and red oaks burned 3× were ultimately 13 and 23 cm shorter those burned 1× ($P < 0.01$ and 0.03, respectively), but white oaks and red maple were similar between the burn treatments ($P = 0.18$ and 0.40, respectively).

Mean seedling basal diameter and total height measured in 2007 were strongly correlated (Fig. 5). Except for sassafras, the regression slopes increased and y-intercepts generally decreased with burn number (Table 3) suggesting a greater increase in height for every unit increase in basal diameter for seedlings burned repeatedly than seedlings unburned or burned 1×.

Lower canopy cover in 2006 was also significantly correlated with higher annual height growth (based on plot means) in 2007 (Fig. 6) for all seedling groups except sassafras ($P = 0.24$). This correlation was strongest for red maple ($R^2 = 0.84$), but was based on 10 plots, compared to 33 for both oaks.

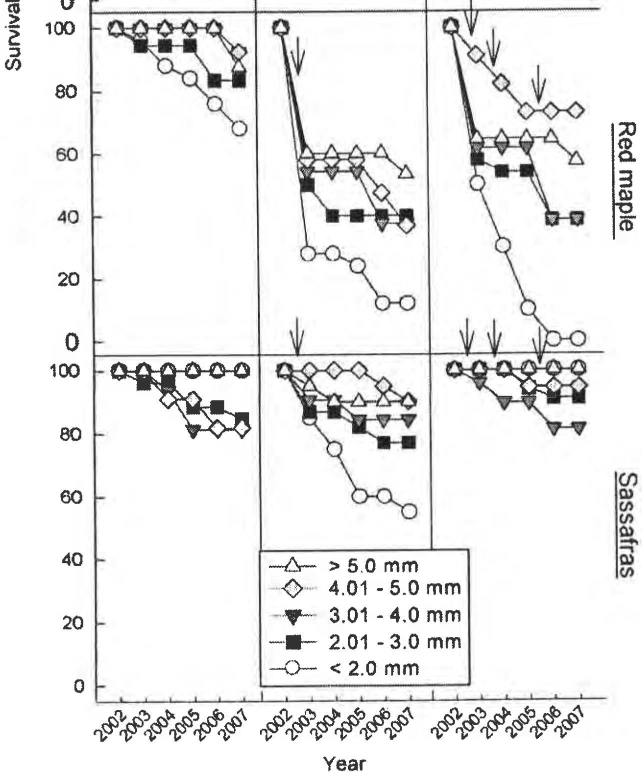


Fig. 3. Seedling survival as a function of initial basal diameter size class tallied across sites. Arrows indicate burn. *Note*: Symbols for small sassafras (<2 mm) overlap with those for large sassafras.

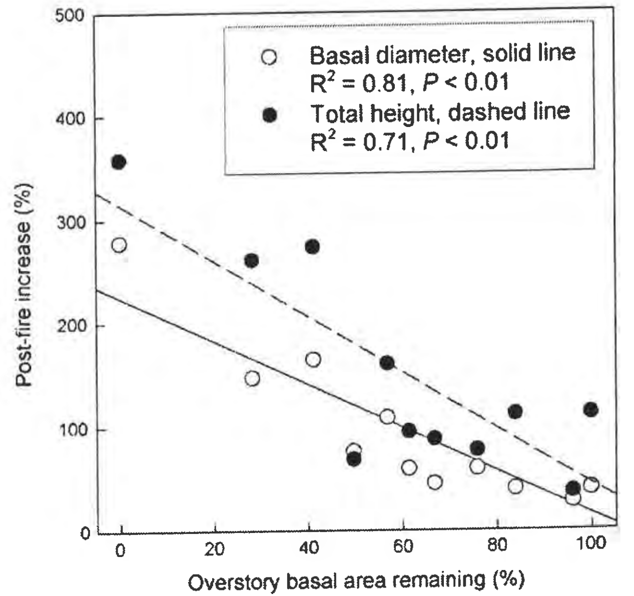


Fig. 4. Remaining overstory (%basal area) and red oak basal diameter and total height increases from 2002 to 2007 at Wolf Pen intermediate plots burned 1×.

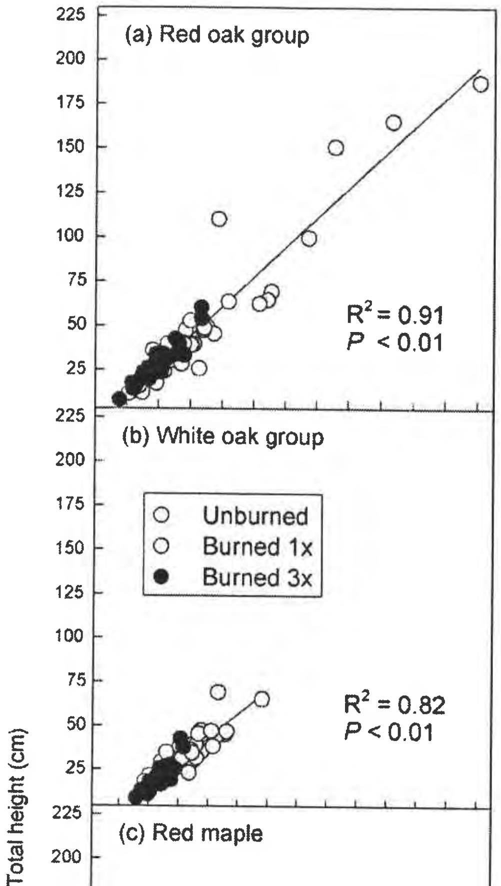


Table 3
Linear regression results of basal diameter vs. total height based on plot means in 2007

Seedling group	Trt	n (# plots)	R^2	P-value	Eqn of Line
Red oaks	All	80	0.91	<0.001	$y = 8.40x - 6.48$
	Unburned	23	0.87	<0.001	$y = 6.76x - 1.88$
	Burned 1×	30	0.91	<0.001	$y = 8.52x - 5.70$
	Burned 3×	27	0.89	<0.001	$y = 8.63x - 6.22$
White oaks	All	72	0.82	<0.001	$y = 6.80x + 2.12$
	Unburned	22	0.82	<0.001	$y = 5.94x + 5.71$
	Burned 1×	26	0.77	<0.001	$y = 6.90x + 2.03$
	Burned 3×	24	0.76	<0.001	$y = 8.89x - 4.02$
Red maple	All	22	0.87	<0.001	$y = 9.59x - 3.01$
	Unburned	7	0.82	0.005	$y = 8.56x - 2.92$
	Burned 1×	9	0.94	<0.001	$y = 10.47x - 6.88$
	Burned 3×	6	0.67	0.045	$y = 12.03x - 6.21$
Sassafras	All	35	0.9	<0.001	$y = 11.36x - 7.54$
	Unburned	7	0.98	<0.001	$y = 12.12x - 11.92$
	Burned 1×	16	0.89	<0.001	$y = 11.09x - 9.09$
	Burned 3×	12	0.94	<0.001	$y = 14.73x - 23.29$

4. Discussion

Our results on unburned sites exemplify the current status of oak regeneration beneath mostly closed canopies in eastern deciduous forests. Without fire, canopy cover was 90–94%, and oak seedlings exhibited high mortality and slow growth. Oak total height increased only 2 cm yr^{-1}, and basal diameter increased 0.1 and 0.3 mm yr^{-1} for white and red oak subgenera, respectively. At this rate, seedlings currently 30 cm tall would not reach 1 m high for another 35 yr. Lorimer et al. (1994) measured slow growth (4–6 cm yr^{-1}) of natural oak seedlings in mature stands in

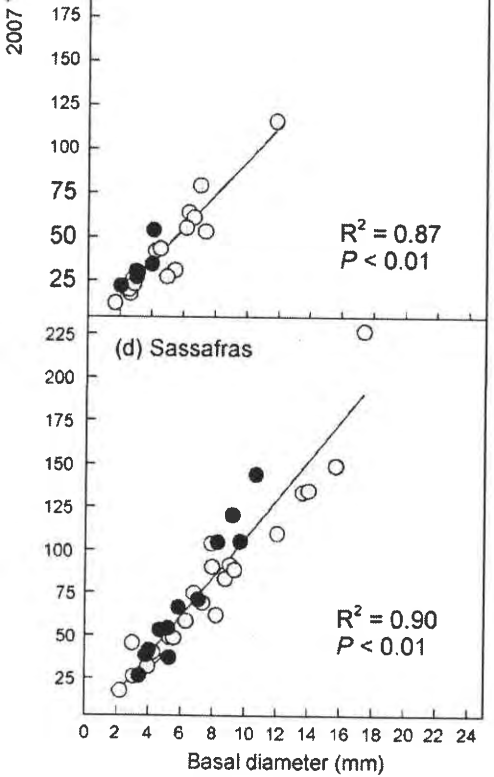
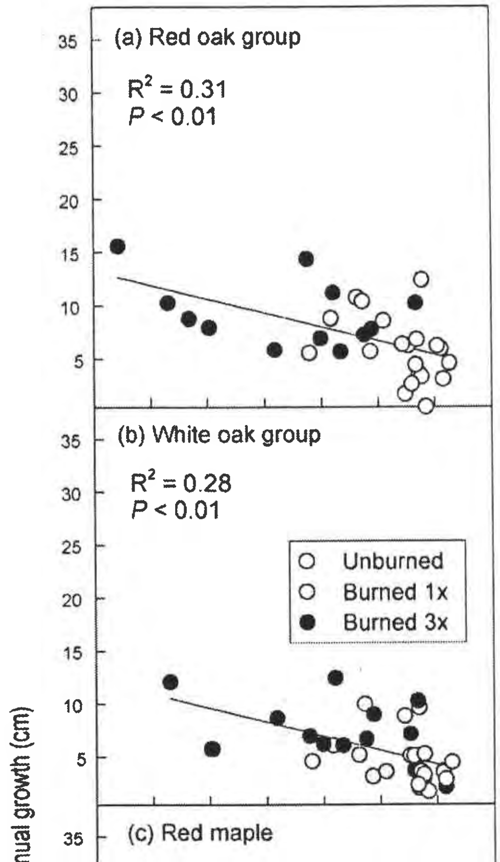


Fig. 5. Basal diameter vs. total height of each seedling group based on plot means in 2007. Trendlines, R^2, and P-values are for all treatments combined. For individual treatments see Table 3.

Wisconsin, but even these rates were 2–3× faster than those measured here. Slow growth underneath a dense canopy is not uncommon (Crow, 1992; Dey and Parker, 1996), and previous determinations of root age suggest oak seedlings can persist in the understory on drier sites in the absence of disturbance for 30–50 yr (Sander, 1972). The consequences of slow growth and high mortality under a mature, undisturbed canopy become especially apparent when compared to red maple and sassafras, which exhibited annual height and basal diameter growth 1.5–2.5× faster than oaks. This trend is the essence of the oak regeneration problem in eastern U.S. forests, and relatively better growth and survival of fire-sensitive, shade-tolerant species have been extensively documented by other researchers in nearby regions (Abrams and Downs, 1990; Abrams and Nowacki, 1992; Arthur et al., 1998; Blankenship and Arthur, 2006).

We hypothesized that prescribed fire would enhance oak regeneration by increasing understory light and decreasing growth and survival of competitor species, and that multiple burns conducted frequently would more effectively create these conditions. In this study, single and repeated fires temporarily increased understory light, but canopy cover rebounded by the subsequent growing season. This transitory effect following the initial disturbance may have resulted from prolific sprouting and light occlusion. For example, Chiang et al. (2005), working nearby, correlated rapid light depletion with increased stem density in the shrub stratum, primarily from red maple stump sprouting, and found multiple fires did not decrease post-fire sprouting. A similar pattern of temporarily decreased canopy cover also followed the first and third burn on our sites; the second burn was mild (Table 1), likely from reduced fuel loads due to the prior year's burning, and consequently, changes in canopy cover were relatively small. Importantly, sites burned 3× ultimately had 5–7% lower canopy cover compared to those unburned or burned 1×,



suggesting a cumulative effect of frequent, repeated burns on understory light.

Both single and repeated fires decreased survival of red maple seedlings. Because this species has epigeal germination, dormant buds along the stem's base are often above the soil surface, making them more susceptible to mortality from high burn temperatures than oaks (Brose and Van Lear, 2004). This could lead to decreased sprouting ability (Brose et al., 2006), especially among smaller seedlings, and could partially account for the extremely high red maple mortality we measured on sites burned 1× which experienced high burn temperatures. Red maple also had high mortality on sub-mesic sites several years post-burn, which may reflect a gradual depletion of belowground resources following resprouting, as species with non-conservative growth strategies often have lower root reserves (Huddle and Pallardy, 1999). Importantly, repeated burning did no better at reducing red maple survival than one burn.

Fires did not reduce the growth of surviving red maple compared to those unburned. Red maple is a highly adaptable "super-generalist" (Abrams, 1998), with characteristics of both early and late successional species, that thrives in open, recently disturbed places as well as in the shade of the forest canopy (Sipe and Bazzaz, 1994). Following a disturbance which increases understory light, red maple quickly produces new leaves, which have low construction and maintenance costs because they are thin with few secondary compounds (Nagel et al., 2002). Thus, as long as red maple seedlings have sufficient belowground resources to support re-building aboveground tissues post-fire, they will be able to rapidly utilize available light.

Both single and repeated burns led to a prolific growth response in sassafras and had virtually no effect on survival. Dey and Hartman (2005) measured high sassafras survival (91%) even after

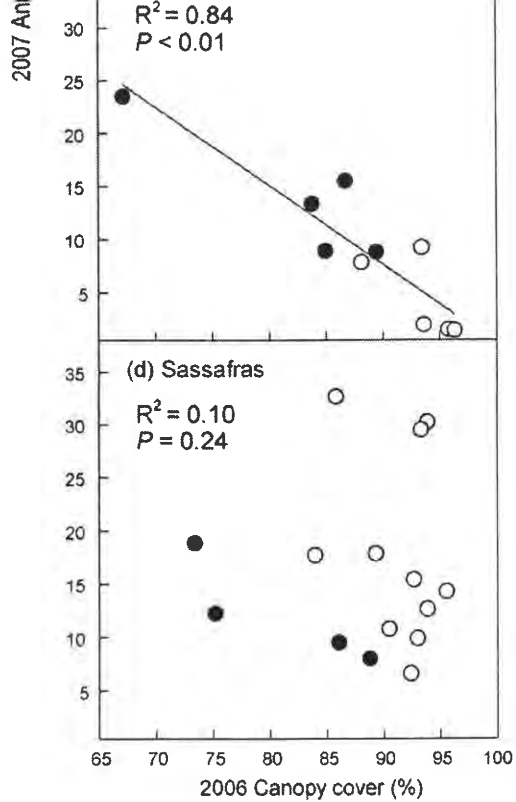


Fig. 6. 2007 seedling growth (plot means) vs. 2006 canopy cover at Buck Creek plots only. Trendlines, R^2, and P-values are for all treatments combined.

four burns, and similar to findings reported here, found survival did not correlate with initial basal diameter. Early studies examining the growth habits of this species describe it as highly adaptable on a variety of soils due primarily to extensive root suckering (Duncan, 1935). Root networks could provide a continual carbon source (Loehl, 2000) and allow efficient re-building of fire-damaged tissues. If parent plants subsidize carbon, this could also explain sassafras survival being independent of initial basal diameter and greater height growth per unit increase in basal diameter compared to other seedlings. Additionally, sassafras roots typically grow 15–50 cm deep (Duncan, 1935), which could protect them from mild, dormant season burns. Sassafras dominance may eventually decrease as individual stems self-thin. However, several studies have shown increased oak seedling survival and growth after removing competing understory and subcanopy species (Loftis, 1990b; Lorimer et al., 1994). Thus, at this critical stage in oak development, the occurrence of a thick sassafras understory could have negative effects on growth of co-occurring oak, primarily via light occlusion.

Despite temporarily increased light and decreased red maple survival after single and repeated fires, oak survival and growth generally remained similar to or lower than on unburned controls. Upland oaks are generally considered "stress-tolerators" (*sensu* Grime, 1977); thus, they are adapted to relatively stable conditions, put considerable photosynthate into storage rather than growth, and do not change their phenotype rapidly when exposed to altered conditions or resources (Dey and Parker, 1996). While oaks often require high light environments for growth and survival (Johnson et al., 2002), their ability to effectively capture a transitory increase in light is limited by their relatively non-plastic growth strategy. In this study, lower canopy cover was positively correlated with higher annual height growth of oaks the subsequent year, and oaks burned 3× had greater height growth per unit increase in basal diameter compared to those unburned or burned 1×. However, slopes of both regressions were relatively low for oaks, suggesting light levels are still insufficient to generate significant height growth, and competing species are better adapted for rapidly utilizing this new resource.

Notably, oak's inflexible growth strategy is a major reason why researchers often report successful oak regeneration following a naturally large canopy opening (Rentch et al., 2003) and why some suggest prescribed fires be conducted following silvicultural canopy manipulations, which can provide long-term changes in understory light. For instance, Brose et al. (1999) found that medium to high-intensity growing season fires conducted 2–4 yr after a shelterwood that removed 50% of the basal area increased oak abundance and stocking. A need for long-term light increases may also explain why the greatest increases in red oak seedling development occurred on sites burned 1×, where a subset of plots experienced high temperatures and high mortality of both understory competitors and overstory trees. While these results were limited to a few plots, they are consistent with previous studies that high-intensity fires in mature stands serve to improve oak regeneration (Swan, 1970; Moser et al., 1996).

Generally, though, prescribed fires in this study did not place oaks in a better competitive position, which may reflect the relatively small pre-burn stature of the oak seedlings. Basal diameter often correlates with root biomass (Jacobs et al., 2005), which affects ability to survive fire (Brose and Van Lear, 2004) and eventually allocate photosynthate to stem growth following top-kill (Lorimer, 1993). However, even when a canopy opening provides sufficiently high and long-lasting light, oak seedlings must be relatively large (basal diameters >1.9 cm; Brose et al., 2006) prior to burning in order to be competitive post-fire. Initial mean basal diameter of oak seedlings in this study was small (<4 mm), and while fire had some positive impacts on red oak protected from fire and can provide carbon sources necessary for resprouting following top-kill. While oaks are generally considered fire-adapted, pre-burn seedling stature appeared especially important. White oaks, with lower initial basal diameters and potentially lower root mass, experienced high mortality and reduced growth following prescribed fire. In contrast, high burn temperatures and consequently high overstory mortality on several plots burned 1× promoted red oak seedling growth and led to survival higher or equivalent to competitors. Notably, these seedlings, predominantly on drier sites, were also larger prior to burning. These results, as well as the relatively minor effects of the mild burns of 2004, exemplify the patchy character of fire and consequent effects on seedlings. In summary, prescribed fires produced few positive effects on oak seedling development due to transitory effects on understory light, minimal impacts on survival and growth of co-occurring competitors, the small pre-burn stature of oak seedlings, and the unpredictable nature of fire.

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and while fire had some positive impacts on red oak seedling development, their diameters remained <7 mm. Thus, further growth development would be necessary for these seedlings to remain competitive following future canopy openings. Small pre-burn stature could also explain why burning was especially detrimental to white oaks. At study initiation, half as many white oaks than red oaks had diameters >5 mm (41 compared to 85 seedlings). Additionally, many chestnut oak (*Q. montana* L.) seedlings on a nearby ridge had hollow roots and lower root mass compared to scarlet oak (*Q. coccinea* Muenchh) and red maple (Chiang, 2002). If seedlings on our sites had similarly low root mass, this could lead to poor sprouting ability and survival following fire and partially explain why white oaks had greater post-burn mortality even among larger diameter classes compared to red oaks.

Although not measured in this study, pre-burn seedling age could also be an important determinant of post-fire oak seedling development. Recent work by Dillaway and Stringer (2007) suggests that oak seedlings residing in the understory in a suppressed state for considerable periods may be physiologically unable to respond to increases in light (even high light provided by a release), as seedlings with older root systems (>8 yr) had lower soluble non-structural carbohydrates, thus less potential vigor.

In conclusion, single and repeated prescribed fires over a 6-yr period in these deciduous forests of eastern Kentucky produced variable results. The generalist red maple exhibited high post-burn mortality following a burn with high temperatures, presumably due to damage to dormant buds, but fire did not affect the growth of surviving red maple, likely due to this species' plastic morphology which allows rapid utilization of newly available resources. Sassafras, which expands clonally via root suckers, was virtually unaffected by single and multiple fires. This species produces extensive belowground root networks which are mostly

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