Foliar morphology and chemistry of upland oaks, red maple, and sassafras seedlings in response to single and repeated prescribed fires

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Abstract: Managers increasingly use prescribed fire in oak forests to decrease fire-sensitive species, increase understory light, and improve oak (*Quercus* spp.) regeneration. To better understand woody seedling response to burning, single and repeated (3×) prescribed fires were implemented over 6 years (2002–2007) in eastern Kentucky, and leaf traits of red (*Erythrobalanus* spp.) and white oaks (*Leucobalanus* spp.) were compared with competitors red maple (*Acer rubrum* L.) and sassafras (*Sassafras albidum* (Nutt.) Nees). Burned seedlings had higher total leaf area (TLA) because of two to three times higher TLA of sassafras. Leaf mass per area (LMA) and leaf N content per area (N_{area}) increased postfire but were independent of seedling identity. Canopy openness during 2006, which was lower on unburned sites (4%–8%) compared with those burned 1× (4%–16%) and 3× (7%–33%), was positively correlated with sassafras TLA, oak and sassafras N_{area}, and LMA of all seedling groups the subsequent year. In 2007, TLA, LMA, and N_{area} were positively correlated with basal diameter of all groups but most significantly for sassafras and red maple. These findings indicate that low-intensity, early growing season prescribed fire can alter seedling leaf characteristics, but not in a manner that enhances oak seedling leaf traits relative to their competitors red maple and sassafras.

Résumé : Les aménagistes utilisent de plus en plus le brûlage dirigé dans les forêts de chênes pour éliminer les espèces sensibles au feu, augmenter la lumière en sous-étage et améliorer la régénération du chêne (*Quercus* spp.). Pour mieux comprendre la réaction des semis ligneux au brûlage, des brûlages uniques et répétés (3×) ont été effectués sur une période de 6 ans (2002–2007) dans l'est du Kentucky et les caractères des feuilles des chênes rouges (*Erythrobalanus* spp.) et blancs (*Leucobalanus* spp.) ont été comparés à ceux des espèces compétitrices : l'érable rouge (*Acer rubrum* L.) et le sassafras officinal (*Sassafras albidum* (Nutt.) Nees). Les semis brûlés avaient une surface foliaire totale (SFT) plus élevée à cause de la SFT du sassafras qui est 2–3× plus élevée. La masse foliaire spécifique (MFS) et la teneur en N foliaire par unité de surface ($N_{surf.}$) ont augmenté après le passage du feu peu importe l'espèce de semis. L'ouverture de la canopée en 2006, qui était plus faible dans les stations non brûlées (4 % – 8 %), comparativement à celle des stations brûlées 1× (4 % – 16 %) et 3× (7 % – 33 %), était positivement corrélée avec la SFT du sassafras, la teneur en $N_{surf.}$ du chêne et du sassafras ainsi qu'avec la MFS de tous les groupes de semis l'année suivante. En 2007, la SFT, la MFS et la teneur en $N_{surf.}$ étaient positivement corrélées avec le diamètre basal de tous les groupes, mais la corrélation était la plus significative dans le cas du sassafras et de l'érable rouge. Ces résultats indiquent qu'un brûlage dirigé de faible intensité effectué au début de la saison de croissance peut modifier les caractéristiques des feuilles, mais pas de façon à améliorer les caractères des feuilles des semis de chêne relativement aux espèces compétitrices, c'est-à-dire l'érable rouge et le sassafras.

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Introduction

Fire suppression in historically oak-dominated forests of the eastern US has facilitated the spread of fire-sensitive tree species leading to low understory light (Abrams 1992). Moderately shade-tolerant oaks (*Quercus* spp.; Burns and Honkala 1990) are competitively inferior under a thick midstory or understory and often experience regeneration failure (Lorimer et al. 1994). Without periodic disturbance, some researchers predict conversion of many forest stands from predominantly oaks to shade-tolerant, fire-sensitive species such as red and sugar maple (*Acer rubrum* L. and *Acer saccharum* Marshall, respectively; e.g., Nowacki and Abrams 2008), which have already increased in density and dominance in many stands (McEwan et al. 2005). Even with disturbance, shade-intolerant species of seed origin, like yellow poplar (*Liriodendron tulipifera* L.), and well-established shade-tolerant regeneration (Van Lear et al. 2000) often outcompete understory oaks whose available resources have been suppressed by an extensive period of low light (Abrams 1992). Importantly, a canopy shift away from upland oaks has numerous ecological consequences, as many wildlife species consume acorns, and oaks have strong influences on community dynamics and ecosystem processes (McShea et al. 2007).

Current management efforts increasingly use prescribed fire with the goal of decreasing competition from fire-

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sensitive species, increasing understory light by removing canopy trees and subcanopy vegetation, and promoting oak seedling growth and development. Burning has been hypothesized to preferentially enhance oak regeneration because oaks have hypogeal germination, which places dormant buds below the soil surface and minimizes fire damage, and a conservative growth strategy, which promotes a large belowground root system that facilitates regrowth after top kill (Brose and Van Lear 2004). In contrast, many co-occurring fire-sensitive species have epigeal germination and a nonconservative growth strategy, which promotes height over diameter growth (Lorimer et al. 1994), but often exposes dormant buds to high burn temperatures (Brose and Van Lear 2004). Thus, oaks are expected to have greater survival and growth in postfire environments thereby enhancing their ability to compete with co-occurring woody seedlings following a subsequent canopy release (Barnes and Van Lear 1998). However, studies evaluating prescribed fire effects on oak regeneration report variable outcomes (Brose et al. 2006) and frequently indicate that fires without any other silvicultural manipulation (*i*) fail to systematically kill oak seedling competitors, including those species typically classified as "fire intolerant" (e.g., Albrecht and McCarthy 2006), (*ii*) produce moderate to significant mortality of oak seedlings, especially those of smaller size classes (e.g., Dey and Hartman 2005), and (*iii*) create only modest or temporary changes in light intensity (e.g., Hutchinson et al. 2005).

In an associated seedling population study (Alexander et al. 2008), prescribed fire effects on survival and growth of seedling sprouts (initial seedling height ≤60 cm) of upland oak were compared with two competitors, red maple and sassafras. White oaks (*Leucobalanus* spp.) experienced high mortality and reduced growth following prescribed fire, possibly because of relatively low initial basal diameters (<4 mm). In contrast, high burn temperatures (surface temperatures of ~600 °C) and high overstory mortality (>50% basal area reduction) on several plots burned 1× promoted growth of red oak (*Erythrobalanus* spp.) seedlings and led to survival higher or equivalent to that of competitors. Notably, these seedlings, predominantly on drier sites, were larger prior to burning (basal diameter ≥6 mm). Among competitors, fires negatively impacted red maple survival, with negligible effects on growth of surviving seedlings, but fires promoted sassafras growth with virtually no impact on survival. Furthermore, understory light increased temporarily, and at study cessation, mean canopy openness on plots burned 3× was ~15%, about 6% higher than sites unburned or burned 1×.

These and other findings suggest that fire effects on oak regeneration are inherently complicated, because fire influences woody seedling dynamics at many levels. Also, species may have different growth strategies and life history traits that produce a variety of seedling responses to fire disturbances. Fire acts directly on seedling survival through heating effects, and as mentioned earlier, differences in bud exposure among species can have a large impact on relative postfire survival (Brose and Van Lear 2004). Fire also can alter environmental conditions and resource availability, such as understory light, which often coincide with changes in other abiotic conditions (e.g., water availability, soil temperature; Naidu and DeLucia 1997). While nitrogen (N) can be lost during fires because of volatilization at relatively low temperatures (200 °C; White et al. 1973), a meta-analysis by Wan et al. (2001) reported increased soil availability of NH_4^+ and NO_3^- across ecosystems and fire types for up to 1 year following fire. These increases have been linked to pyrolysis of organic matter, postfire changes in soil moisture and temperature that stimulate N mineralization, and leaching of N from the forest floor into underlying soils following fire (Wan et al. 2001). If surviving seedlings have differing abilities to acclimate to a new set of abiotic conditions and respond rapidly to transitory increases in available resources, even small changes in light or N availability could impact seedling growth and competitive stature in postfire environments. Further, the removal of aboveground tissues by fire may also alter leaf physiology because of changes in root:shoot dynamics (e.g., Reich et al. 1990). Following late-spring fires in Wisconsin, Kruger and Reich (1997*b*) measured an increase in foliar leaf N per unit area and photosynthetic capacity of three temperate species despite finding no increase in postfire soil N or water availability. The magnitude of these responses differed among species, suggesting variable consequences of fire-induced resprouting on seedling growth and recovery following fire (Kruger and Reich 1997*a*, 1997*c*).

To gain further insight regarding the underlying mechanisms affecting relative differences in seedling growth previously observed in postfire environments, this study focused on woody seedling response at the leaf level. While whole-plant responses are the best indicators of how different seedlings will respond to altered environmental conditions (Kruger and Reich 1997*a*, 1997*b*, 1997*c*; Naidu and DeLucia 1997), previous work has indicated that leaf traits also can provide additional information regarding plant ecophysiological response to abiotic factors (Abrams et al. 1994), mechanisms affecting growth patterns and competitive interactions (Reich et. al. 1990), and leaf susceptibility to herbivory (Rieske 2002). Specifically, single and repeated (3×) prescribed fires were implemented over a 6 year period (2002–2007) in mature, second-growth forests in eastern Kentucky, and preburn and postburn changes in total leaf area (TLA), leaf mass per unit area (LMA), N content per unit leaf area (N_{area}), foliar carbon (C) and N concentrations, and leaf C/N ratios were quantified annually in oak and co-occurring competitor seedlings of red maple and sassafras. To evaluate the role of understory light, these leaf characteristics were examined in 2007 in relation to the previous year's canopy openness. Leaf characteristics in 2007 also were used to assess potential links among seedling size, measured as basal diameter, and foliar morphology and chemistry. We hypothesized that seedlings would acclimate to postfire changes in understory light by increasing their TLA and (or) LMA, as these leaf traits have been previously shown to be effective strategies for increasing light interception and assimilation (DeLucia et al. 1998; Aranda et al. 2004). We predicted that if fire increased soil N availability or altered root:shoot dynamics, this would be reflected in foliar N concentration (Reich et al. 1990). We further hypothesized that these responses would be more pronounced in oak seedlings compared with red maple and sassafras seedlings, because oak's conservative growth strategy pro-

motes a large belowground root reserve, providing energy to offset costs associated with building new leaves with high C or N.

Methods

Study area

Leaf parameters were measured in forest stands within the Cumberland Ranger District of the Daniel Boone National Forest (DBNF) of eastern Kentucky. Prior to burn treatment, the forest was mature, second-growth, regenerating ~80–100 years ago following logging. Overstory (stems ≥10 cm diameter at breast height (DBH)) preburn basal area averaged 20–30 $m^2 \cdot ha^{-1}$. Oak, including scarlet (*Quercus coccinea* Muenchh), black (*Quercus velutina* Lam.), northern red (*Quercus rubra* L.), white (*Quercus alba* L.), and chestnut oak (*Quercus montana* L.), and hickory, including pignut (*Carya glabra* (Mill.) Sweet var. *glabra*), bitternut (*Carya cordiformis* (Wangenh.) K. Koch), and mockernut (*Carya tomentosa* (Poir.) Nutt.), dominated overstory composition. Midstory (2–10 cm DBH) dominants were red and sugar maple (*A. rubrum* and *A. saccharum*, respectively), downy serviceberry (*Amelanchier arborea* (Michx. f.) Fern), black gum (*Nyssa sylvatica* Marshall), and sourwood (*Oxydendrum arboreum* (L.) DC.). Few oaks (<3%) contributed to midstory stem density, while red maple's density was ~45%.

Climate is generally humid, temperate, and continental. Mean annual air temperature is 12.8 °C, with mild winters and hot summers (mean daily temperature = 0.5 °C and 24 °C in January and July, respectively). Annual rainfall (122 cm) is equally distributed throughout the year (Foster and Conner 2001). Estimates of the Palmer drought severity index (PDSI) obtained for the region from the National Climatic Data Center (http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp#) indicated strong interannual swings in moisture availability during the study. PDSI for 2002 (0.56) indicated an "incipient wet spell", followed by "moderately wet" (2.71) and "extremely wet" (4.03) years in 2003 and 2004, respectively. The PDSI during 2005 and 2006 was "normal" (0.02 and –0.20, respectively), while 2007 was a "moderate drought" (–2.47).

Experimental design

The overall study design consisted of three burn treatments (unburned, burned 1×, and burned 3×), each within three replicate study sites (Buck Creek, Chestnut Cliffs, and Wolf Pen). Study sites were within an 18 km^2 area and were ~200–300 ha each. Each burn treatment encompassed 58–116 ha (see Alexander et al. 2008, for more detail) and contained 10–12 plots. Plots were chosen using a grid overlaid on a topographic map and encompassed a variety of aspects, slopes (often exceeding 60%), and elevations (260–360 m). Each plot was parallel to topographic contours and 10 m wide × 40 m long. Because of the logistical constraints associated with leaf-level measurements, the current study used only one site (Buck Creek; 230 ha) within the larger study. This study site contained a total of 33 plots (10 unburned, 11 burned 1×, 12 burned 3×). While each burn treatment within this site contained replication at the plot level, analysis of plot data generated a pseudoreplicated design, because fire could not be applied to each plot individually. Thus, results cannot be generalized beyond Buck Creek; however, it seems reasonable that these findings are representative of the other two sites given their similar variability in aspect, slope, elevation, preburn basal area, soil type, and landscape position (Table 1). Additionally, forest stands within all treatments and study sites were mature, second-growth, originating ~80–100 years ago following extensive logging, and showed similar dominance of overstory and midstory vegetation (see Study area description).

Prescribed fires

Fires were ignited by the US Forest Service using either drip torches and (or) helicopter ignition. Sites burned 3× were burned in spring 2003, 2004, and 2006, while those burned 1× were burned in spring 2003. All burns were between March 26 and April 16, when air temperatures were 20–27 °C, and relative humidity was 23%–45% (see Alexander et al. 2008 for further details). Flame height and spread rates (i.e., fire intensity) were not measured because of the large size and highly dissected topography of the study sites and concern for personnel safety. However, variability in fire temperature was quantified using pyrometers at four locations within each plot (see Loucks et al. 2008 for methodology). Fire temperatures at each site within the larger study and potential effects on whole seedling growth and survival are reported in Alexander et al. (2008).

Across the Buck Creek plots, surface fire temperatures (mean ± SD) varied with year. In 2003, temperatures were 473 ± 182 °C and 563 ± 77 °C at plots burned 1× and 3×, respectively. Greater variability at plots burned 1× resulted from a single plot, which had comparatively low temperatures. During 2004, only 50% of plots burned, likely a result of greater fuel discontinuity because of burning only 1 year prior, leading to a mean (±SD) surface burn temperature of only 149 ± 172 °C. During 2006, burn temperatures were more homogeneous (529 ± 45 °C). Importantly, burn temperatures during the 2003 fire were significantly and positively ($P < 0.001$; $R^2 = 0.49$) correlated with canopy openness measured the following summer, while temperatures in subsequent fires were not, suggesting initial surface fire temperatures and associated fire behavior strongly influenced understory light.

Seedling leaf traits

Preburn (June 2002), seedlings of oaks and their most predominant competitors were selected from the pool of advance regeneration (98% were ≤60 cm height), permanently tagged with a unique identification number, and mapped as part of a long-term seedling population study to assess survival and growth in response to prescribed fire (Alexander et al. 2008). All seedlings were well established, with a mean height of 21.5 ± 14.1 cm, and they were visually inspected at the root collar to ensure they were independent seedlings. No true seedlings (i.e., seedlings that had not been previously top-killed and resprouted) were observed or selected.

Within a 2 week period during the growing season (early July to mid-August) from 2002 to 2007, seedlings of species represented in each plot as part of the seedling population study were selected within a 10 m radius of the outside periphery of the permanent population plot for determination

Table 1. Mean (SE) plot characteristics within each study site included in the overall experimental design.

Parameter	Buck Creek			Chestnut Cliffs			Wolf Pen		
	Unburned	Burned 1×	Burned 3×	Unburned	Burned 1×	Burned 3×	Unburned	Burned 1×	Burned 3×
Slope (%)	43.6 (20.0)	44.1 (18.5)	37.7 (22.0)	37.0 (10.1)	42.2 (14.6)	33.7 (20.4)	42.2 (12.8)	51.8 (21.6)	37.8 (20.8)
Elevation (m)	326 (23)	331 (23)	319 (42)	321 (21)	307 (27)	306 (19)	315 (16)	307 (32)	314 (23)
Overstory basal area (m^2)	23.1 (5.6)	20.1 (4.5)	24.4 (10.0)	18.9 (7.4)	20.3 (7.8)	20.6 (11.8)	30.9 (9.6)	26.0 (8.8)	23.3 (11.5)
Geologic substrate	S/DS	S/DS	S/DS/LS	S/DS/LS	S/DS/LS	S/DS/LS	S/DS	S/SS	S/SS
Landscape position	3 SM, 3 INT, 4 SX	4 SM, 3 INT, 4 SX	0 SM, 8 INT, 4 SX	6 SM, 4 INT, 0 SX	3 SM, 6 INT, 1 SX	4 SM, 5 INT, 1 SX	8 SM, 2 INT, 0 SX	1 SM, 7 INT, 4 SX	4 SM, 3 INT, 1 SX

Note: Leaf characteristics were measured only within the Buck Creek study site. Overstory basal area refers to trees ≥10 cm diameter at breast height (DBH). Geologic substrate classifications were acquired from the Salt Lick USGS Quadrangle: S, siltstone; DS, dolomite shale; SS, sandstone; LS, limestone. Landscape positions are based on McNab et al. (2007). SM, submesic; INT, intermediate; SX, subxeric.

of leaf characteristics and basal diameter. Treatments, plots, and species were sampled randomly, resulting in a different order each year. During 2002, only one seedling of each species at each plot was selected; this sampling approach was modified in remaining years, and two seedlings of each species at each plot were selected. Selected seedlings were of similar size as those in the long-term seedling population study and usually included a total of three species: one species of the dominant white oak (*Leucobalanus* spp.), one species of the dominant red oak (*Erythrobalanus* spp.), and the most abundant competitor species, either red maple (*A. rubrum*), sugar maple (*A. saccharum*), sassafras (*Sassafras albidum* (Nutt.) Nees), white ash (*Fraxinus americana* L.), hickory (*Carya* spp.), or eastern redbud (*Cercis canadensis* L.). However, this sampling scheme was occasionally modified because more than a single red or white oak species dominated a plot, or we needed a combination of two or more species per plot to generate sufficient seedlings for the population study. In these instances, we sampled four species per plot. Overall, this sampling scheme resulted in >200 seedlings sampled annually (33 plots × ~3–4 species × 2 seedlings per species). *Leucobalanus* spp. included white oak (*Q. alba*; 706 seedlings·ha^{-1}) and chestnut oak (*Q. montana*; 1302 seedlings·ha^{-1}), and *Erythrobalanus* spp. included black oak (*Q. velutina*; 677 seedlings·ha^{-1}), scarlet oak (*Q. coccinea*; 421 seedlings·ha^{-1}), and northern red oak (*Q. rubra*; 189 seedlings·ha^{-1}). Sassafras and red maple were by far the most dominant competitor species (~3900 and 3600 seedlings·ha^{-1}, respectively).

The number of seedlings top-killed by each fire varied among burns. Of the seedlings within the larger population study which survived the initial (2003) fire at Buck Creek, ~95% experienced top kill and resprouting. Because the 2004 fire was relatively mild, only 29% of surviving seedlings had undergone top kill and resprouting. However, the 2006 fire top-killed 95% of surviving seedlings. These levels of top kill were relatively consistent among study sites. Importantly, burn temperature and seedling survival among all three sites were not correlated (Alexander et al. 2008).

For each selected seedling, two perpendicular measurements of basal diameter were made with a digital caliper where the stem exited the soil. The number of fully expanded leaves on each seedling was counted, and TLA was obtained on each seedling by scanning every fully expanded leaf with a portable leaf area meter (LI-3000A area meter, LI-COR, Inc., Lincoln, Nebraska). To determine seedling LMA and assess foliar C and N, several mature, fully expanded leaves with minimum insect or browse damage were excised from the upper portions of every measured seedling, placed in a dampened paper towel, and transferred in a prelabeled plastic bag to the laboratory, where they were stored at 4 °C until further analysis. Within 2 days, leaves were cleaned of any debris, scanned on a leaf area meter (LI-3100 area meter, LI-COR, Inc.), and placed in a 60 °C oven. Leaves were dried to a constant mass, and within 1 week, weighed to obtain dry mass. LMA for each seedling was calculated by dividing the dry mass of the leaves extracted from each seedling by their laboratory-determined leaf area. A 1 cm diameter disk from one randomly selected dried leaf per seedling was removed (taking care to avoid the mid-vein), weighed to the nearest 0.0001 g, and stored

at 60 °C until analysis for C and N concentrations using a Leco CN 2000 analyzer (Leco Corporation, St. Joseph, Michigan). Leaf N content per unit area (N_{area}) was calculated by multiplying foliar N concentration by LMA.

Canopy cover

Understory light was estimated annually during July by acquiring hemispherical photographs of canopy openness; however, only data from 2006 and 2007 were used in this study. To account for within-plot light variability, photographs were obtained at three locations (10, 20, and 30 m) along the bottom axis of each sampling plot, and because light conditions from a "seedling's perspective" were desired, photographs were acquired 80 cm above the forest floor. To limit uneven exposure due to direct sunlight, photograph acquisition was restricted to either before sunrise, after sunset, or when overcast. A digital camera attached to a Nikon FC-E8 183° fisheye converter and placed on a Delta-T Devices self-leveling mount positioned toward magnetic N was used to take all photographs. Because hemispherical photographs were only used to assess canopy openness and not other light estimates which require solar tracks to be superimposed, this camera orientation was used only as a means of ensuring similar camera placement from year to year. The entire hemispherical image was analyzed for all estimations. Digital photographs were initially processed with Adobe Photoshop to remove lighted direction markers and maximize contrast between open sky and canopy. Images were then analyzed in random order using HemiView 2.1 and evaluated three times by a single analyst to produce an average canopy cover value for each location at each plot.

Statistics

For statistical analyses, oak seedlings were pooled into red or white oak subgenera, and comparisons of leaf traits were made between these two oak subgenera, red maple, and sassafras. Additionally, when two seedlings per species per plot were sampled, the mean of the measurements was used for statistical analyses. We focused on these competitor species because of their dominance across plots and because other species measured did not have sufficient replication at the treatment level to provide meaningful results. We grouped oaks into subgenera because initial evaluations of potential species-specific differences proved minimal. Chestnut and white oak did not significantly differ with regard to any parameter. Among red oaks, black and scarlet oak were generally statistically similar, while northern red oak had greater foliar N, lower C/N ratios, lower LMA, and higher N_{area} than these other two red oaks. However, when we evaluated the impact of northern red oak on overall trends by removing these data from statistical analyses, we found no influence, likely because northern red oak represented only a small portion of the overall data set. Thus, we chose to leave this species in the data set for all analyses. All future references to the four seedling types analyzed (red oaks, white oaks, red maple, and sassafras) will be as "seedling groups". Sample sizes differed among these four seedling groups. Both red and white oak species were sampled on every plot, and occasionally we sampled more than one red or white oak species on a single plot (see Methods: Seedling leaf traits), while red maple and sassafras were only sampled on plots where they were the dominant competitor. Thus, annual sample sizes per treatment ranged from 14 to 16, 10 to 12, 2 to 6, and 5 to 6 for red oaks, white oaks, red maple, and sassafras, respectively, yielding a total annual sample size across treatments of 44, 33, 11, and 16, respectively. In each year but 2002, these sample sizes were based on the mean of the two seedlings sampled per species per plot.

Plots were treated as the experimental unit, and mean seedling data for each plot were analyzed by ANOVA as a three-way factorial (main effects = burn treatment, year, and seedling group) with repeated measures using the MIXED procedure of SAS version 8 (SAS Institute Inc., Cary, North Carolina, USA). While the use of only one sampling site generates a pseudoreplicated design (Hurlbert 1984) and violates the underlying assumption of independence of experimental units, the use of an ANOVA seemed reasonable given the similar preburn variability in aspect, slope, elevation, preburn basal area, and soil type within each of the Buck Creek treatments (Table 1). Most importantly, analysis of preburn leaf data indicated no treatment differences, suggesting observed postburn differences were truly due to burning and not to some other effect. There was some variability in landscape position (calculated according to McNab et al. 2007) among treatments, but previous analyses of landscape position indicated little to no effect on litter mass or woody fuels (Loucks et al. 2008), no effect on canopy openness and seedling growth, and only limited effects on seedling survival (Alexander et al. 2008). Since there were no detectable landscape position effects on seedling total height, annual height growth, or basal diameter, it is unlikely that this variable accounted for the observed postburn differences in leaf characteristics.

TLA data did not meet the underlying assumptions of homogeneity of variance and normality and were log-transformed prior to analyses. 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, the Satterthwaite method was used to estimate degrees of freedom. For all significant effects, least squares means were compared via a post hoc Fischer's LSD test to determine differences among means at $\alpha = 0.05$.

Because the temperate species evaluated usually have determinate growth and we rarely observed a second flush on seedlings, we expected light from any particular year to be most influential on leaf parameters the subsequent year, although light within a particular year likely influences leaf parameters as well. Thus, we explored relationships between burn-induced changes in canopy openness in 2006 and leaf parameters in 2007 as well as canopy openness and leaf parameters in 2007 using linear regression and correlation procedures (PROC REG of SAS). Comparison of the two analyses indicated similar findings, likely because canopy openness in 2006 was tightly correlated with that in 2007 ($R^2 = 0.80$; $P < 0.001$). However, there were more significant correlations and stronger trends (i.e., higher R^2) using 2006 canopy openness; thus, we only present those findings here. Notably, the calculation of canopy openness at the plot level probably fails to incorporate the complete light environment experienced by a seedling because it does not con-

sider sunflecks (Rich et al. 1999) and was not assessed immediately above each individual seedling.

Seedling basal diameter is an important indicator of seedling belowground resources (Jacobs et al. 2005), and in a companion study (Alexander et al. 2008), exhibited a strong positive correlation with seedling total height among seedling groups and treatments. To determine if leaf parameters correlated with this measurement of seedling size, we evaluated 2007 seedling basal diameter and leaf parameters. Differences between slopes and *y*-intercepts of trendlines for each seedling group were evaluated by ANCOVA.

Results

TLA

Unburned seedlings had significantly lower mean TLA (0.024 m^2) than those burned 1× (0.033 m^2) and 3× (0.034 m^2; $P = 0.003$ and $P < 0.001$, respectively), but burning 3× did not significantly alter TLA compared with burning only 1× ($P = 0.76$; Fig. 1). There was also a steady and significant ($P < 0.001$) increase in TLA from 2002 (0.023 m^2) to 2007 (0.063 m^2), which was independent of treatment ($P = 0.07$), but varied by seedling group ($P < 0.001$). By 2007, red oaks had greater TLA (0.069 m^2) than red maple (0.042 m^2; $P = 0.03$) and white oaks (0.040 m^2; $P = 0.001$), but sassafras had two to four times greater TLA (0.139 m^2) than all other seedling groups ($P < 0.001$ for all). There was no treatment × seedling group effect on TLA ($P = 0.30$), suggesting species-specific effects were not sufficiently large to generate significant variation by treatment. However, burned sassafras seedlings clearly had higher TLA than other seedling groups from 2005 to 2007, and our counts of leaf number (data not shown) indicated that this was due to increased leaf number and not to greater area per leaf.

LMA

Seedlings burned 3× had significantly greater LMA (52.1 $g \cdot m^{-2}$) than those burned 1× (46.2 $g \cdot m^{-2}$; $P < 0.001$), which were significantly greater than those unburned (41.9 $g \cdot m^{-2}$; $P = 0.002$), but these treatment effects were independent of seedling group ($P = 0.35$; Fig. 2). Preburn, LMA was statistically similar across treatments ($P > 0.05$ for all), but after the first burn in 2003 and continuing throughout the study, unburned seedlings had significantly lower LMA than seedlings burned 3× ($P < 0.01$ for all years). In contrast, seedlings burned 1× had significantly higher LMA from those unburned only during the first year postburn ($P < 0.001$).

There were interannual fluctuations in LMA that varied with seedling group ($P < 0.001$). Across treatments, LMA of red maple and sassafras seedlings peaked in 2004, the wettest year. Red maple LMA was also relatively high in 2007, a very dry year. LMA of both oaks peaked in 2003 on burn sites, which led to significantly higher LMA of oak seedlings in 2003 than in 2002 ($P < 0.01$). This effect was temporary, and oaks in 2004 no longer significantly differed from those in 2002 ($P = 0.95$).

Foliar N

There was no overall treatment effect on seedling foliar N concentration ($P = 0.86$; Fig. 3), although this parameter

Fig. 1. Mean annual total leaf area ± SE for each seedling group across each treatment. Seedlings burned 1× were burned in spring 2003, and those burned 3× were burned in spring 2003, 2004, and 2006.

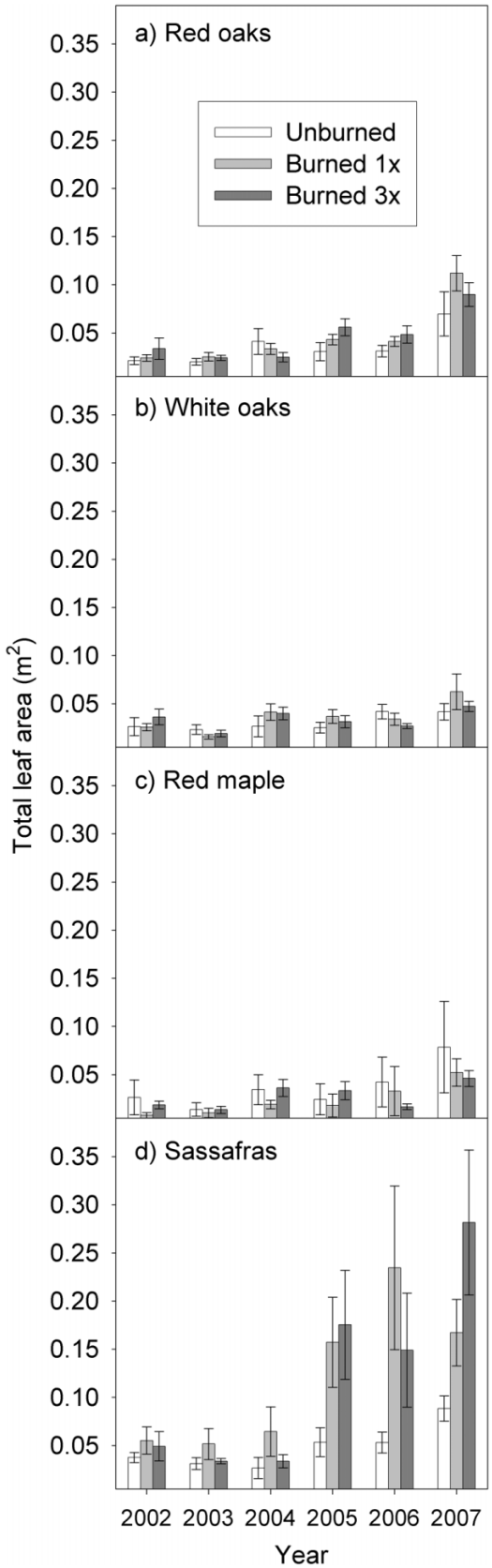


Fig. 2. Mean leaf mass per unit area ± SE for each seedling group across each treatment. Seedlings burned 1× were burned in spring 2003, and those burned 3× were burned in spring 2003, 2004, and 2006.

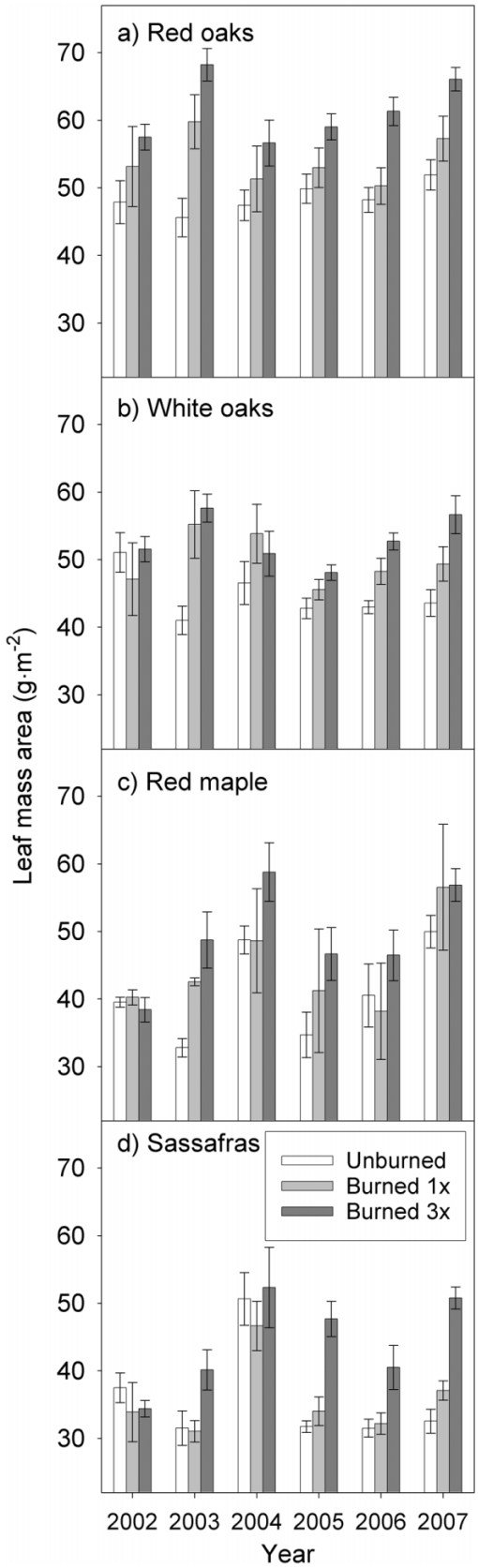
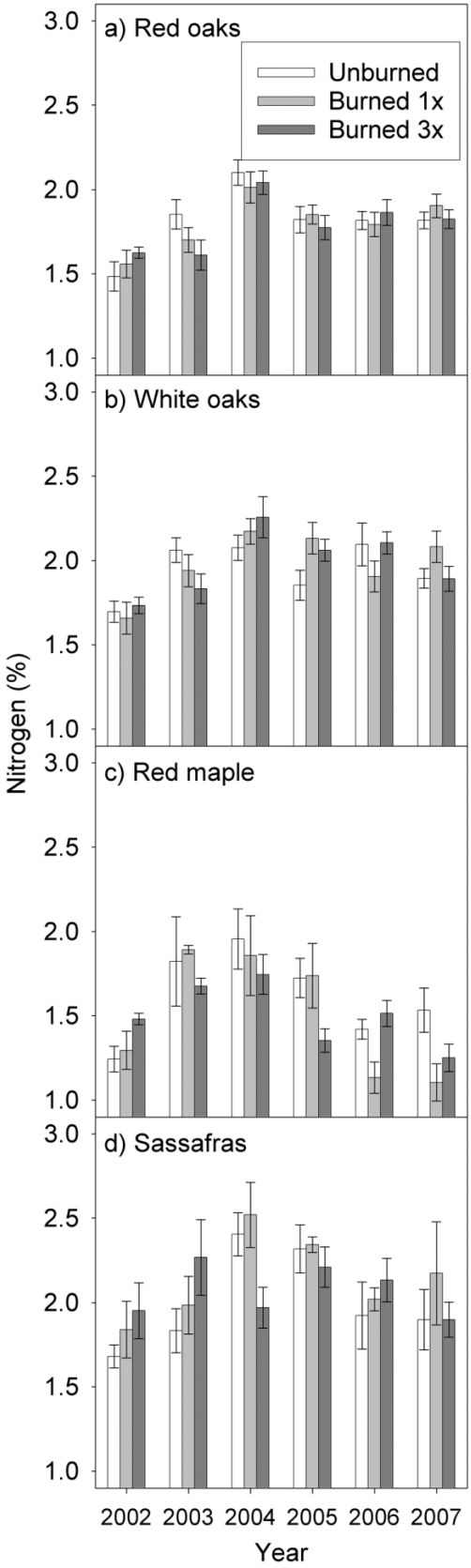


Fig. 3. Mean foliar nitrogen concentration ± SE for each seedling group across each treatment. Seedlings burned 1× were burned in spring 2003, and those burned 3× were burned in spring 2003, 2004, and 2006.



varied among seedling groups ($P < 0.001$). Red maple had the lowest overall foliar N concentration (1.54%). Red and white oaks were intermediate (1.80% and 1.97%, respectively), and sassafras was highest (2.07%). There was significant interannual variability ($P < 0.001$), apparently driven by changes in precipitation. Across seedling groups, N concentrations were high in 2004 and low in 2002 and 2007. There also were significant treatment × year ($P = 0.008$) and treatment × year × seedling group ($P = 0.02$) effects, which appeared to be driven by decreased foliar N concentrations of red maple seedlings in 2007 on burned sites.

When expressed as foliar N content per unit area (N_{area}; Fig. 4), there were significant burn effects ($P < 0.001$). Seedlings burned 3× had significantly greater N_{area} (0.95 g·m^{-2}) than those burned 1× (0.85 g·m^{-2}; $P = 0.001$), which were significantly greater than those unburned (0.77 g·m^{-2}; $P < 0.001$). Burn effects depended on year ($P < 0.001$), but did not vary with seedling group ($P = 0.30$). Immediately after the first fire, seedlings burned 1× and 3× had significantly higher N_{area} (0.87 and 0.96 g·m^{-2}, respectively) than those unburned (0.70 g·m^{-2}; $P = 0.002$ and $P < 0.001$, respectively). Burned seedlings also had statistically higher N_{area} than preburn ($P < 0.001$ for both burn treatments), while unburned seedlings did not ($P = 0.19$), suggesting that despite some preburn variability, changes in N_{area} of burned seedlings from 2002 to 2003 were due to burning and not to some other factor common across treatments. Burn effects were not consistent throughout the years, as N_{area} of unburned seedlings was statistically similar to those burned 1× ($P = 0.33$) and 3× ($P = 0.09$) in 2004, during or following relatively wet years, but differed again in 2005 and 2007. In 2006, immediately following the third burn on plots burned 3×, N_{area} of seedlings burned 3× was higher than those unburned and burned 1× ($P < 0.001$ for both), which were not significantly different from each other ($P = 0.96$). All seedling groups except red and white oaks differed from one another ($P < 0.01$), but these effects depended on sampling year ($P < 0.001$). Notably, in 2004, N_{area} of all seedling groups was similar, but in all other years, oaks had higher N_{area} than both red maple and sassafras.

In 2007, mean N_{area} within each seedling group from each plot was positively correlated with mean LMA, except for red maple ($R^2 = 0.15$; $P = 0.24$). This trend was stronger for red and white oaks ($R^2 = 0.70$ and 0.72, respectively; $P < 0.001$ for both) than sassafras ($R^2 = 0.33$; $P = 0.02$). Oaks also exhibited a greater increase in N_{area} per unit change in LMA than sassafras, as indicated by higher slopes (slope = 2.1 and 1.8 for red and white oaks, respectively, compared with sassafras slope = 1.4; $P < 0.001$ for all comparisons) of the regression trendlines.

Foliar C

There were significant treatment effects on foliar C concentration ($P = 0.009$; Fig. 5), but these were independent of year ($P = 0.25$) and seedling group ($P = 0.99$). Seedlings burned 3× had slightly higher mean C concentration (49.1%) compared with those burned 1× (48.8%; $P = 0.02$) and unburned (48.2%; $P = 0.005$). Seedling group also affected foliar C concentration ($P < 0.01$). Red maple and sassafras did not significantly differ ($P = 0.22$) but had higher

Fig. 4. Mean foliar nitrogen content per unit area (N_{area}) ± SE for each seedling group across each treatment. Seedlings burned 1× were burned in spring 2003, and those burned 3× were burned in spring 2003, 2004, and 2006.

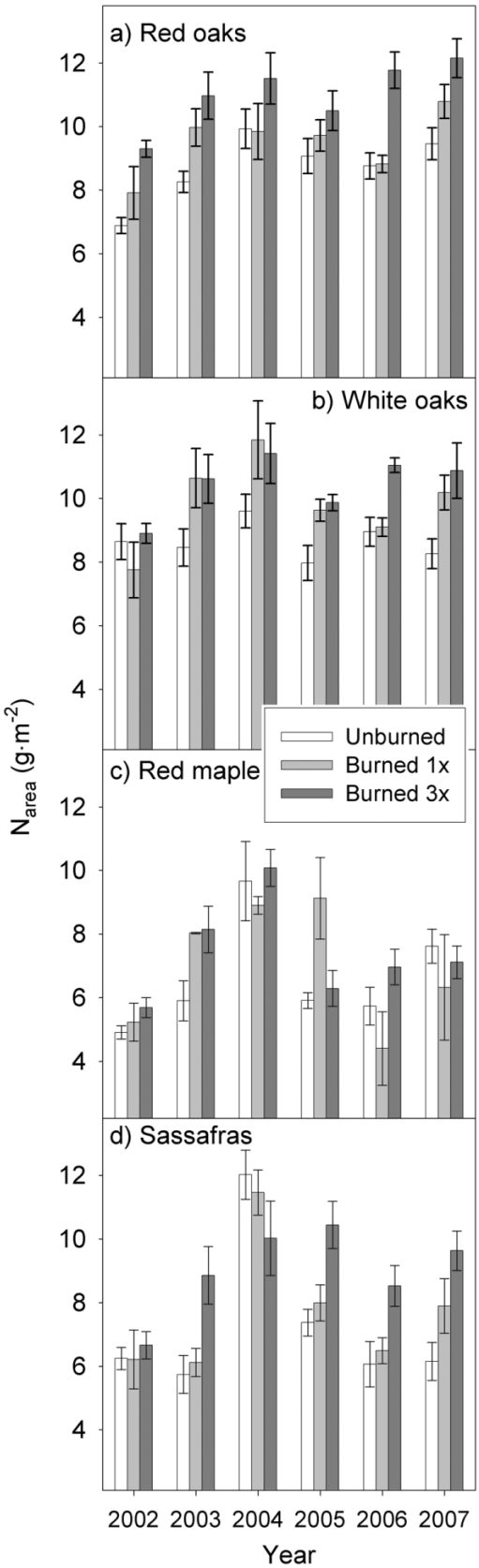
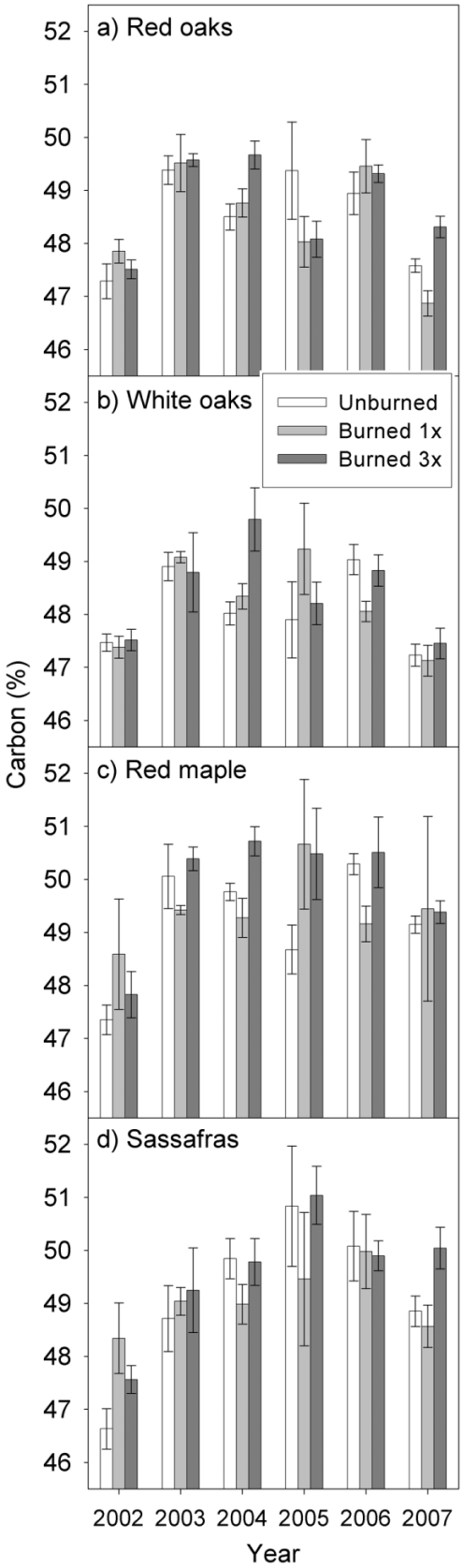


Fig. 5. Mean foliar carbon concentration ± SE for each seedling group across each treatment. Seedlings burned 1× were burned in spring 2003, and those burned 3× were burned in spring 2003, 2004, and 2006.



C (49.5% and 49.3%, respectively) than red (48.5%) and white (48.3%) oaks, which were not significantly different ($P = 0.09$). C also varied by year ($P < 0.001$) and was lowest during or following dry years 2002 and 2007.

Mean foliar C concentration in 2007 exhibited a positive linear correlation with mean LMA for red oaks ($R^2 = 0.31$; $P < 0.001$), red maple ($R^2 = 0.42$; $P = 0.03$), and sassafras ($R^2 = 0.56$; $P < 0.001$), but not white oaks ($R^2 = 0.00$; $P = 0.65$). Trendline slopes were not significantly different among species ($P = 0.92$), but *y*-intercepts differed ($P < 0.001$) because at any given C concentrations, red oak LMA was higher than red maple, which was higher than sassafras.

C/N ratios

There was no treatment effect on seedling foliar C/N ($P = 0.64$), but all seedling groups significantly differed from each other ($P < 0.01$ for all comparisons). C/N was highest for red maple (33.2), intermediate for oaks (red = 27.7, white = 25.2), and lowest for sassafras (24.8). There also was significant interannual variation ($P < 0.01$). Foliar C/N decreased from 30.6 in 2002, a relatively dry year, to 24.5 in 2004, a very wet year, and increased again to 28.9 in 2007, a very dry year. Among seedling groups, red maples had the greatest variability in C/N ratios, with C/N occasionally being higher on burned plots, but mean values were never statistically different among treatments ($P > 0.05$)

Canopy cover and leaf parameters

Several trends emerged for mean leaf parameters measured at each plot in 2007 and regressed against previous year mean canopy openness (expressed as open sky; Fig. 6). Mean TLA of sassafras increased significantly ($R^2 = 0.41$; $P = 0.0007$) with increasing open sky, whereas mean LMA increased significantly ($P < 0.001$ for all) with increasing understory light for all seedling groups (R^2 ranged from 0.40 for white oaks to 0.79 for sassafras). The regression slopes indicated a similar increase in LMA per unit increase in open sky for both oaks and sassafras (slope = 0.09–1.0; $P = 0.09$), but *y*-intercepts significantly differed ($P < 0.001$) such that LMA at any given light level was highest for red oaks, intermediate for white oaks, and lowest for sassafras. The slope of red maple's trendline (0.70) was ~30% lower than other seedling groups ($P < 0.05$ for all comparisons), although the *y*-intercept was similar to red oaks. Notably, the response of red oak LMA with increasing open sky tended to be more curvilinear, reaching a maximum LMA of 70 $g \cdot m^{-2}$ at open sky values ≥15%, suggesting a physiological limit to this foliar parameter. Foliar N concentration and C/N ratios did not vary with understory light for any seedling group, but N_{area} significantly increased with increasing light for red oaks ($R^2 = 0.31$; $P < 0.001$), white oaks ($R^2 = 0.17$; $P = 0.02$), and marginally for sassafras ($R^2 = 0.23$; $P = 0.05$), but not red maple ($R^2 = 0.06$; $P = 0.47$). Foliar C concentration of red oaks ($R^2 = 0.25$; $P = 0.003$) and sassafras ($R^2 = 0.30$; $P = 0.03$) increased significantly with increasing light.

Leaf parameters and seedling size

Seedling size, measured as basal diameter, exhibited positive linear correlations with several leaf traits. TLA was strongly and positively correlated (R^2 ranged from 0.57 for

Fig. 6. Mean leaf parameters for each plot in 2007 regressed against 2006 open sky (%) for each seedling group across each treatment. Seedlings burned 1× were burned in spring 2003, and those burned 3× were burned in spring 2003, 2004, and 2006.

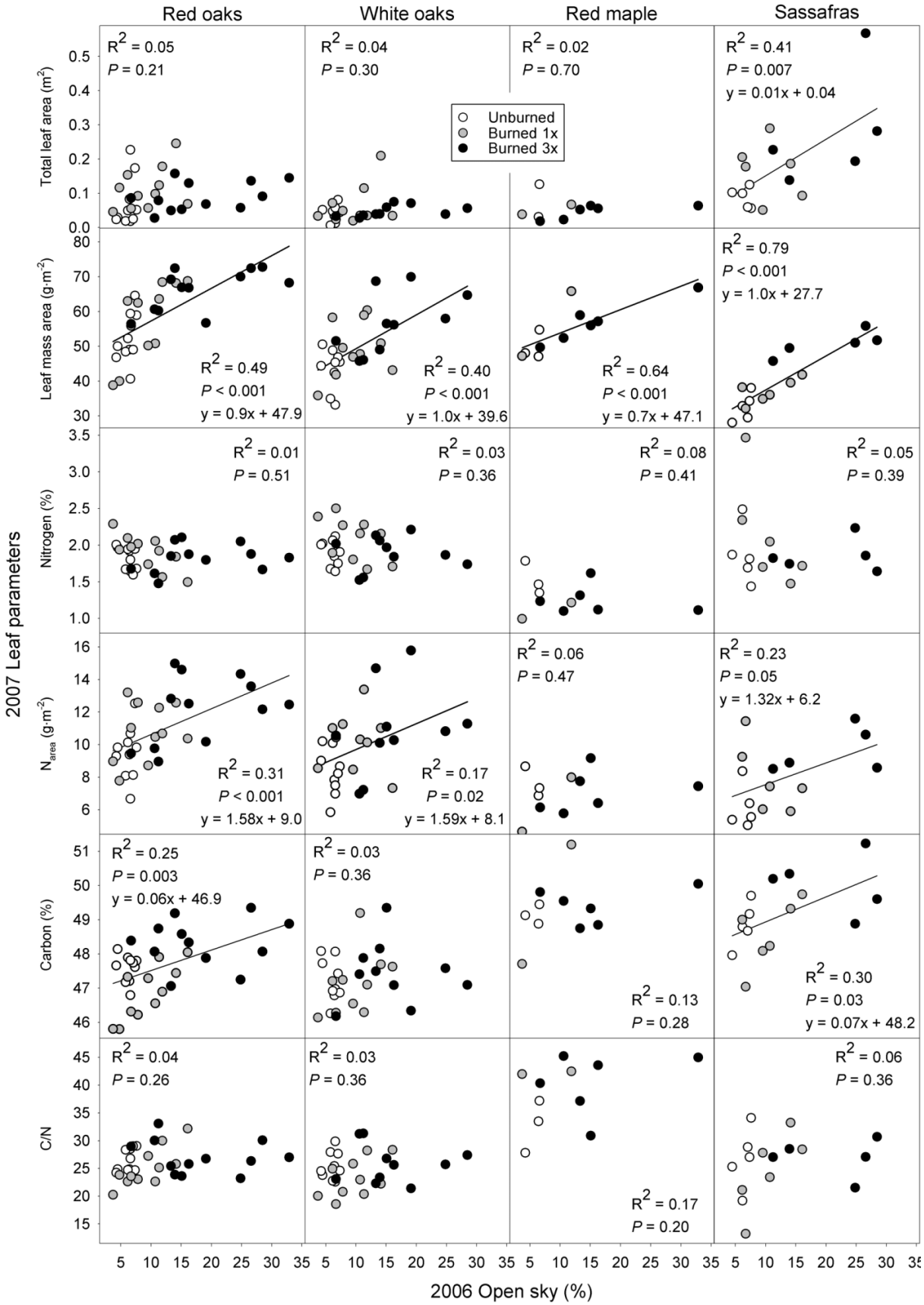
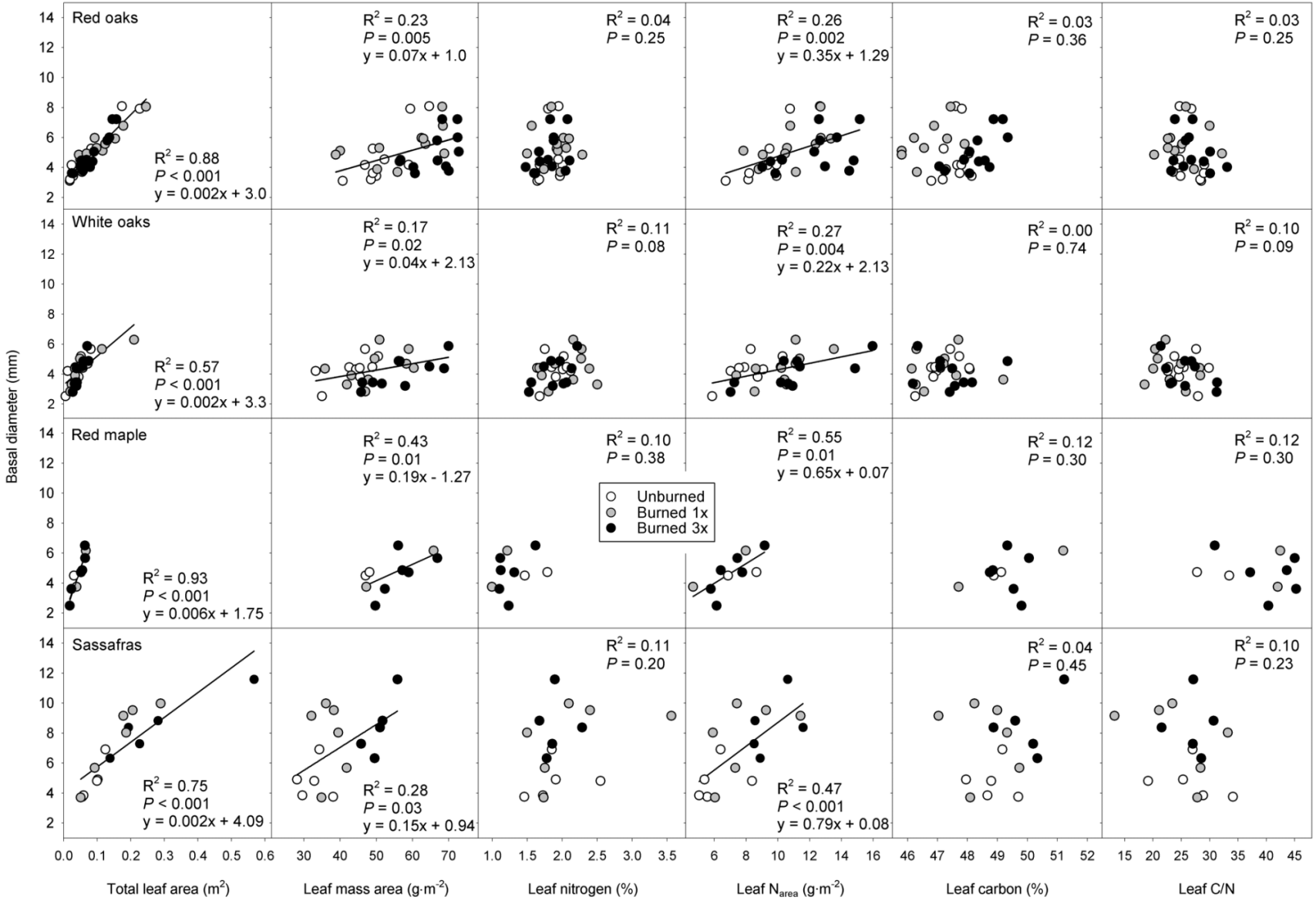


Fig. 7. Mean leaf parameters for each plot regressed against mean basal diameter in 2007 for each seedling group across each treatment. Seedlings burned 1× were burned in spring 2003, and those burned 3× were burned in spring 2003, 2004, and 2006.



white oaks to 0.93 for red maple; $P < 0.001$ for all) with seedling basal diameter across seedling groups (Fig. 7). The response was strongest for red maple, which had a slope three times steeper (0.0063) than oak or sassafras, whose slopes were statistically similar ($P = 0.09$). LMA and N_{area} were both positively correlated with basal diameter, but these trends were strongest for red maple and sassafras ($R^2 = 0.55$ and 0.47, respectively), which had slopes two to four times greater than either oak. C and N concentrations and foliar C/N exhibited no correlations with basal diameters.

Discussion

In postfire environments, surviving oak seedlings have been hypothesized to gain a competitive edge, because their conservative growth strategy promotes development of belowground resources that facilitate regrowth after top kill (Larsen and Johnson 1998). Yet, leaf alterations that promote interception and assimilation of newly available understory light, minimize water loss, or reflect an increase in soil N availability, could have important growth advantages. Overall, changes in oak seedling leaf characteristics in response to fire and the reflection of these leaf changes in growth parameters and competitive stature depend on a combination of interacting factors: (*i*) extent and duration of change in the abiotic parameter, (*ii*) inherent phenotypic plasticity and ability to capture a transitory versus a long-lived change in resource availability, and (*iii*) relative response of competing seedlings.

One way a seedling could take advantage of increased understory light postfire is to increase TLA. In this study, burned seedlings had higher TLA than those unburned, but this was driven by a two- to three-fold increase in sassafras leaf area. This response was not magnified by repeated burning, and was related to understory light, as indicated by the positive correlation of sassafras TLA in 2007 with previous year canopy openness. Increasing TLA in response to increased light could be an effective strategy for early successional, shade-intolerant species like sassafras, which are not adapted to residing in the understory for long periods. In contrast, later successional species may not use this strategy because leaves are costly, both in terms of construction and maintenance (Barthod and Epron 2005), and low leaf area may confer a lower risk of herbivory and exposure to pathogens (DeLucia et al. 1998) and lower susceptibility to temporary decreases in water availability. Increasing TLA for some species may only be advantageous under conditions of permanently high light availability. For example, Sipe and Bazzaz (1995) found that red maple produced many small leaves generating higher TLA ($\sim$350 cm^2) in large gaps (300 m^2), but in small gaps (75 m^2), leaf area was four times smaller ($\sim$80 cm^2), which is comparable to values obtained here. While fire led to a wide range of canopy openness among plots, large canopy gaps were relatively rare and often only temporary because of prolific resprouting of midstory and understory species, which occluded a substantial portion of understory light the subsequent year (M. Arthur and D. Loftis, unpublished data).

Seedlings could also increase their photosynthetic capacity in response to postfire conditions by increasing their LMA and foliar N_{area}. Increased LMA with increased irradiance is common (e.g., Ellsworth and Reich 1993) and represents a change in a seedling's leaf dry-mass investment per unit of area available for light interception, resulting from either increased leaf thickness or density (Wright et al. 2004). These changes can increase the concentration of N-rich photosynthetic enzymes like RUBISCO and lead to a concomitant increase in N_{area}, which often leads to greater photosynthetic capacity per unit leaf area (Ellsworth and Reich 1993) and return of assimilated C (Aranda et al. 2004). N_{area} can also increase in response to increased foliar N concentrations because of increased soil N availability.

In this study, LMA and N_{area} were higher in burned seedlings, but there were no differences among seedling groups. These changes likely reflect increased understory light, as these parameters were positively correlated with canopy openness. The lack of fire-induced changes in foliar N concentration in this study, and strong correlations of LMA and N_{area}, suggest changes in LMA were responsible for changes in N_{area} in all seedling groups but red maple. Enhanced LMA postfire contrasts with data obtained by both Gilbert et al. (2003) working on a nearby ridge in Kentucky and Reich et al. (1990) in central Wisconsin who found no or few significant differences between LMA of seedlings on burned and unburned sites. Both of these studies evaluated a single burn, and neither reported variations between preburn and postburn understory light, suggesting limited changes in LMA could be due to minimal changes in light.

Increased LMA postfire also could result from changes in foliar C concentration. If fire leads to high evaporative losses through reduced forest floor mass and (or) increased light, seedlings may respond through increased epidermal or cuticle thickness (Ashton and Berlyn 1994), which could increase foliar C concentrations. In this study, LMA was positively correlated with foliar C concentration of red oaks, red maple, and sassafras when considered across treatments. This trend emerged because foliar C tended to increase with burn number. Niinemets et al. (1999) measured increased foliar lignin, a C-rich compound, with increasing light, and suggested that this could be a side effect of light-induced water stress. Adams and Rieske (2003) measured elevated foliar tannins in white oaks on burned sites, presumably from increased light (Dudt and Shure 1994).

We expected foliar N concentration to increase if fire increased soil N availability (Wan et al. 2001) or altered root:shoot dynamics (Kruger and Reich 1997*b*). However, there was a lack of foliar N response to burning. Loucks et al. (2008) measured little burn effects on forest floor organic matter after the 2003 and 2004 fires; thus, these low-intensity fires may not have increased N availability. Alternatively, fire-induced increases in available soil N may have been transitory and dissipated in the 4 month period between burning and sampling. Blankenship and Arthur (1999) measured only a 1 day increase in soil N following a single fire in eastern Kentucky. Gilbert et al. (2003), working in the same study site, found only a 4 month postfire increase in foliar N, which they speculated may have been due to the dilution of foliar N as seedling growth increased in response to fire (Reich et al. 1990).

All seedling groups exhibited positive correlations between basal diameter and TLA, LMA, and N_{area}, but the

trendline slopes were often highest for red maple and sassafras. Differences among seedling groups may result from different costs associated with constructing and maintaining leaves (Nagel et al. 2002; Barthod and Epron 2005). Increased LMA can lead to increased cell lignification (Baruch and Goldstein 1999) and increased epidermal and cuticle thickness (Ashton and Berlyn 1994), which entail investment in costly C molecules. Constructing and maintaining leaves with greater N per unit leaf area is also costly (Poorter and Villar 1997). If leaves already contain high levels of these expensive compounds, as do oak leaves, increased costs could lead to lower gains in photosynthate and consequent ability to invest in growth.

Conclusions

The results presented here represent the second part of a long-term study to assess prescribed fire effects on upland oak and co-occurring woody seedling growth and survival and provide another level of detail to help us understand how and why different woody seedlings respond to postfire conditions in a specific manner. These findings suggest that low-intensity, early growing season fires can alter foliar morphology and chemistry, especially TLA, LMA, and N_{area}, of upland oak and co-occurring competitor seedlings. These changes were often related to altered canopy cover conditions and were positively correlated with increased seedling basal diameter. However, differences in leaf parameters among seedling groups were either minimal or indicated an enhanced response of the competitors red maple and sassafras. Thus, even when oak seedling foliar characteristics responded positively to fire, their competitors performed equivalently or better.

Many of the survival, growth, and leaf-level differences observed in this and the companion study (Alexander et al. 2008) reflected differences in growth strategies and allocation patterns among seedling groups, which are important determinants of phenotypic plasticity and ability to capture a transitory versus a long-lived change in resource availability. Sassafras, an early successional, shade-intolerant species with clonal ramets, consistently exhibited greater survival, total height, and basal diameter growth following fire, and results of this study suggest one way that this species may be able to achieve superior stature is by producing greater TLA and more effectively being able to increase basal diameter with every incremental increase in LMA and N_{area}. Red maple, a "super-generalist" with adaptations to various environments (Abrams 1998), exhibited reduced survival postfire but no alterations in growth. Postfire variations in leaf traits were also comparatively small in this species. Red and white oaks, with their moderate shade tolerance and "stress-tolerator" growth strategy, responded differently to burning. Fires were detrimental to white oak growth and survival, while red oaks had moderate postfire survival and stimulated growth on plots with heavy overstory mortality. Both oak subgenera exhibited increased LMA and N_{area} postfire, but these increases were always similar to red maple and sassafras, and may reflect the relatively high costs of constructing and maintaining oak leaves, which are rich in N and recalcitrant C (Nagel et al. 2002).

The combined findings of the previous and current studies provide further evidence that upland oak seedlings in the deciduous forests of eastern Kentucky are not responding to low-intensity, early growing season prescribed fires, conducted singly or repeatedly, in a manner that consistently places them in a better competitive position. This lends credence to the idea that prescribed fires without silvicultural manipulation may not be an especially effective management tool for enhancing oak regeneration in this region.

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