Prescribed fire affects white oak seedling phytochemistry: implications for insect herbivory

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Abstract

Fire suppresses vegetative competition, increases light penetration and soil nutrients, and is an integral part of the disturbance regime forming the oak (*Quercus*)-dominated forests of eastern North America. Fire can affect plant foliar chemistry through changes in nutrient availability and light intensity, which can influence herbivore feeding patterns. We considered the interactions between fire and oak seedling herbivory by assessing the effects of prescribed fire on white oak (*Quercus alba* L.) foliar chemistry. We hypothesized that fire would provide increased light penetration and added nutrients that would enhance the nutritional status of foliage, thereby leading to greater herbivore pressure.

We compared white oak foliar chemistry and root characteristics of seedlings from once-burned (1998), twice-burned (1996 and 1998), and non-burned sites over 2 years. We also challenged seedlings with supplemental herbivory and measured foliar chemical responses to herbivore pressure. In two separate experiments, native, seasonal, host-adapted lepidopteran herbivores (eastern tent caterpillar, *Malacosoma americana* F., and fall webworm, *Hyphantria cunea* Drury) were caged and allowed to feed on seedlings from burned and non-burned sites on two dates during the 1999 growing season.

We found little difference in plant chemistry among our burn treatments, but sample year strongly influenced our results, perhaps due to fluctuations in soil conditions caused by drought in the post-burn year (1999). Foliar calcium levels were moderately lower in seedlings from burned sites the year of the burn ($P = 0.06$), but this difference disappeared 1 year post-burn. Most phytochemical components were higher in seedlings sampled 1 year post-burn (1999) than in those sampled in the year of the burn (1998). Regardless of burn (site) treatment, caterpillar feeding resulted in foliage with lower concentrations of carbohydrates ($P = 0.0001$), nitrogen ($P = 0.006$), and tannins ($P = 0.06$). Foliar carbohydrates tended to increase within each year, and appeared inversely related to foliar nitrogen and tannins.

Our results do not support the hypothesis that prescribed burning alters white oak seedling phytochemistry, or increases seedling susceptibility to herbivory through bottom-up changes in foliar chemistry, nor do they explain anecdotal accounts of increased herbivory on burned sites.
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1. Introduction

Plant foliar chemistry affects herbivore feeding patterns in a variety of plant systems, including annuals (Kogan and Fischer, 1991), herbaceous perennials (Bowers and Stamp, 1993), and coniferous

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(Wagner, 1988) and deciduous (Scriber and Slansky, 1981) trees. Changes in foliar chemistry may be accompanied by corresponding changes in insect feeding patterns (Faeth, 1985), insect mortality (Hartley and Lawton, 1987), plant morphology (Karban and Myers, 1989), and plant fitness (Whitham and Mopper, 1985; Agrawal, 1998, 1999). Nutrients can influence host selection and feeding patterns for many herbivores, including vertebrates (Danell and Huss-Danell, 1985) and arthropods (Brues, 1920; Thorsteinson, 1960; Scriber and Slansky, 1981). Likewise, foliar defensive compounds have proven equally important in influencing feeding patterns of some vertebrate (McArthur et al., 1993) and arthropod (Fraenkel, 1959; Ehrlich and Raven, 1964; Bernays, 1981; Schultz, 1988) herbivores.

Seasonal changes in herbivory on deciduous oak (*Quercus* spp.) trees employing carbon-based defenses typically correspond to changes in foliar carbohydrates, tannins and nitrogen, and increased foliar toughness (Feeny, 1970; Baldwin and Schultz, 1982). With the exception of foliar carbohydrates, which are usually phagostimulatory (Thorsteinson, 1960; Schoonhoven, 1968, but see Zou and Cates, 1994), these alterations can reduce foliar palatability and suitability to herbivores. The act of herbivory itself may further accelerate seasonal changes in foliar quality in some plants, through both local and systemic induction, resulting in increased tannins and decreased nitrogen (Tuomi et al., 1984; Faeth, 1985; Wold and Marquis, 1997). Plant foliar chemistry can further be influenced by abiotic factors such as fertilization (Hunter and Schultz, 1995), light intensity (Dudt and Shure, 1994), and fire (Reich et al., 1990; Kruger and Reich, 1997a,b; Rieske, in press).

Fire enhances the growth and survival of many hardwood species (Lorimer, 1985; Arthur et al., 1998; Adams and Rieske, 2001) by suppressing competition, and increasing light penetration and soil nutrient availability (Reich et al., 1990; Blankenship and Arthur, 1999), and is crucial for maintaining oak dominance in eastern systems (Abrams, 1992). Fire intensity also affects soil nutrient availability (Stark and Steele, 1977), further affecting foliar nutrients. Reich et al. (1990) and Kruger and Reich (1997a,b) observed a short term increase in nitrogen, potassium, and phosphorus in foliage of northern red oak (*Q. rubra* L.) seedlings following low intensity, spring surface fires. In sites burned by a catastrophic fall wildfire, chestnut oak (*Q. prinus* L.) seedlings showed a transient increase in foliar tannins, presumably due to increased light penetration, as well as enhanced foliar nitrogen for the duration of the following growing season (Rieske, in press).

Hypotheses addressing herbivore-plant relations suggest that there are tradeoffs in plant carbon allocation between growth and defense (Bryant et al., 1993; Herms and Mattson, 1992), which may be alleviated under nutrient-rich conditions (Price, 1991), such as those following fire. Herbivore response to fire-induced changes in foliar chemistry have not been fully investigated, and may be system specific. Considering the potentially diverse effects of fire on oak seedling foliar chemistry, the nutritional suitability of seedlings and their susceptibility to herbivory may be drastically altered.

The advantages of prescribed fire for regeneration of oaks in the hardwood forests of the eastern United States have been documented (Lorimer, 1985), but research examining the role of herbivory in these burned hardwood systems is limited (Adams and Rieske, 2001; Rieske et al., 2002; Rieske, in press). Our objective was to map seasonal changes in white oak foliar chemistry on burned sites, and consider the interactions between fire and herbivory by assessing the relative effects of prescribed fire on seedling foliar chemistry in the context of increased herbivore pressure. Using host-adapted polyphagous lepidopteran defoliators, we challenged white oak seedlings in nutrient-rich burned sites and nutrient-poor, light-limited, non-burned sites with elevated herbivore pressure, and compared phytochemical responses. We hypothesized that the proximate effects of fire, acting as a nutrient source and to increase light availability, would enhance the nutritional status of seedling foliage, ultimately leading to greater herbivore pressure.

2. Methods

Our study was conducted in the Daniel Boone National Forest (DBNF) in southeastern Kentucky (US). We compared seasonal foliar chemistry of white oak seedlings from plots on xeric ridgetops in burned and non-burned forests, and assessed phytochemical responses to elevated herbivore pressure.

2.1. Seasonal foliar chemistry

Sites were established in oak-dominated stands with the following treatments: (1) single year (1x) burn:areas burned in late winter/early spring 1998; (2) multiple-year (2x) burn:late winter/early spring burns in 1996 and 1998, and (3) non-burned controls:areas with no recent history of fire activity. In both years, burns were conducted in conjunction with the prescribed fire management program implemented by the US Forest Service. These fires are cool surface burns of low intensity that consume primarily the previous year's leaf litter, and when possible, use pre-existing features as firelines. Three plots of 40 white oak seedlings were located within each site, for a total of 120 seedlings per site. Within each plot, 20 seedlings were randomly chosen and flagged at the beginning of the 1998 and 1999 growing seasons. We defined a seedling as a small white oak averaging 11.5 cm in height, appearing less than several years old from above-ground investigation, and selected from a limited pool of seedlings found in small groups on the forest floor.

Destructive sampling for phytochemical analysis occurred at approximately 21 day intervals in 1998 (2 June, 16 June, 8 July, and 29 July) and in 1999 (27 May, 10 June, 30 June, and 20 July). Sampling dates in 1999 were coordinated with those in 1998 based on growing degree-day observations. At each interval, five of the 20 pre-selected seedlings in each plot were randomly chosen and destructively sampled.

Leaves from each seedling were removed from the petiole and divided into two groups, one of which was flash frozen in liquid nitrogen for analysis of carbohydrates and tannins, the other of which was oven dried for nutrient analysis. Foliage that was flash frozen was ground into a fine powder using a mortar and pestle, freeze-dried for 36 h (VirTis Freezemobile 12SL, The VirTis Company, Inc., Gradiner, NY), and stored at −80 °C prior to analysis of carbohydrates and tannins. Foliar carbohydrate analysis was conducted with an anthrone/thiourea reagent (Quarmby and Allen, 1989). Foliar tannin levels were analyzed using a radial diffusion assay (Hagerman, 1987), with a protein-based agar to serve as the substrate for tannic acid binding.

The second group of leaves from each seedling were packed in wet paper towels, stored on ice, and returned to the laboratory. Leaf area (LI-3100 Area Meter, LI-COR, Inc., Lincoln, NE) and fresh weight were immediately measured. After a minimum of 6 days drying at 40 °C, dry weight was measured and foliage was ground with a mortar and pestle for nutrient analysis. Foliar nutrients were assessed using the block digestion method of Isaac and Johnson (1976).

Five additional seedlings from each plot were excavated during the dormant season (November 1998 and January 1999) for analysis of root carbohydrates. Seedling height and root length were measured, and root tissue was flash frozen in liquid nitrogen, ground to a fine powder and analyzed for carbohydrate content (Quarmby and Allen, 1989).

2.2. Herbivore manipulation

To assess seedling response to elevated herbivore pressure, we used two sites of multiple-year (2x) burned forest and adjacent non-burned controls. Three plots of white oak seedlings adjacent to those used for phytochemical analysis were designated for herbivore manipulation.

We manipulated herbivory levels by caging lepidopteran defoliators on white oak seedlings, and measured subsequent changes in seedling foliar chemistry on two dates in 1998. For the early-season (1 May) experiment, we used eastern tent caterpillars, *Malacosoma americana* F. (Fam: Lasiocampidae), and for the late season (26 September) experiment we used fall webworm caterpillars, *Hyphantria cunea* Drury (Family: Arctiidae). Both are native, polyphagous defoliators capable of exploiting white oak as a host during the later instars (Drooz, 1985). Cages consisted of fine white cloth mesh completely enclosing each seedling, supported by a wire tomato cage (35 cm × 30.5 cm) and secured at the base and top with binder clips.

On both sampling dates, three white oak seedlings from each plot were randomly designated as herbivore-challenged (caged with caterpillars), and two seedlings were designated as unchallenged controls (caged without caterpillars). Thus, for the first assay, there were two replications of each of the site treatments, burned and non-burned, and two replications of the seedling treatments, herbivore-challenged (caged with caterpillars, $N = 18$) and unchallenged (caged without caterpillars, $N = 12$), for a total of 60

experimental seedlings. Due to problems of accessibility, one site was omitted for the second assay, resulting in a total of 30 experimental seedlings ($N = 18$ herbivore-challenged seedlings, and $N = 12$ unchallenged seedlings).

All caterpillars were field collected, maintained in the laboratory at 23 °C and 16:8 L:D on foliage collected from mature white oak trees, and starved 24 h prior to use in experiments. For each experiment, we adjusted the number of caterpillars and time interval to produce a consistent level of herbivory for each seedling, targeting 50% of seedling leaf tissue removed. For the early-season experiment, we used three, fourth-instar eastern tent caterpillars per seedling over 4 days. For the late season experiment we used seven, fourth-instar fall webworm caterpillars per seedling over 5 days. Herbivory levels were visually assessed at 24–48 h intervals, and when they reached 30–50% on most of the seedlings, caterpillars were removed.

After caterpillars were removed, caged seedlings were sampled for phytochemical analysis. Leaves were excised and foliage from each treatment was pooled according to the level of damage produced by the defoliators. That is, heavily damaged leaves (>60% defoliation) were processed separately from moderately damaged (20–60% defoliation), lightly damaged (<20% defoliation), and undamaged leaves, for each assay date. Carbohydrate and tannin analyses were performed as described previously, and foliar nitrogen levels were measured using a Leco TN-300 nitrogen determinator (Leco Corp., St. Joseph, MI).

2.3. Statistical analysis

Statistical models for seasonal phytochemical data were based upon a split-plot design, with time (assay dates) blocked within site (burn) treatment. Data were analyzed using Proc Mixed (SAS Institute, 1997). Fixed effects included burn treatment and sampling date; the random effect was plot nested within site (burn treatment). All pairwise comparisons were made using a least significant difference (LSD) test. Data presented for foliar carbohydrates and tannins are only from the first and last sampling interval for each respective year.

For the herbivory experiments, treatments were evenly replicated in the first assay, but in the second assay one site was omitted. Because of unequal variances in overall herbivory levels, we used the nonparametric Kolmogorov–Smirnov goodness of fit test (Sokol and Rohlf, 1981) to compare herbivory between seedling treatments (herbivore-challenged versus unchallenged) across both dates and for each individual date. Statistical models were based upon a split-split-plot design, with seedling treatment (caging with and without herbivores) and time (two assay dates) blocked within site (burn) treatment. Fixed variables included burn treatment and sample date. Because there was no correlation between herbivore-damage level and foliar chemistry, phytochemical measurements within each seedling treatment within each plot were averaged prior to statistical analysis. Data were analyzed using Proc Mixed (SAS Institute, 1997) and pairwise comparisons were made using a LSD test.

3. Results

3.1. Seasonal phytochemistry

Foliar carbohydrate concentrations were significantly higher 1 year post-burn (1999) than in the year of the burn (1998) (LSD $F_{1,90} = 165.09$; $P = 0.0001$), but seasonal increases were similar between years (Fig. 1a, 1998: LSD $F_{1,32} = 60.93$; $P = 0.0001$ and 1999: $F_{1,29} = 8.60$; $P = 0.007$). There were no differences in foliar carbohydrates due to burn treatment in either year (Table 1). Similar trends were detected between the 2 years, however, with seedlings from plots in the multiple-year burns having relatively low levels of foliar carbohydrates.

Early-season foliar tannin levels were similar in both years (Fig. 1b), but overall concentrations were significantly higher in the burn year than in the post-burn year (LSD $F_{1,89} = 13.99$; $P = 0.0003$). A significant date by year interaction (LSD $F_{1,88} = 13.48$; $P = 0.0004$) occurred between the 2 years and indicates a marked decline in tannin concentrations during the 1999 growing season (Fig. 1b, LSD $F_{1,33} = 33.47$; $P = 0.0001$), with more constant levels in 1998. Foliar tannins also did not differ between burn treatments (Table 1).

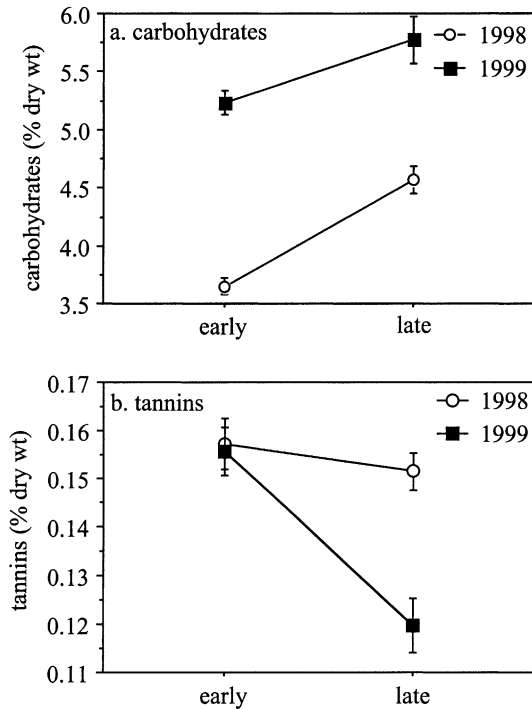Concentrations of most foliar nutrients were higher 1 year post-burn than in the year of the burn, including

Fig. 1. *Q. alba* seedling foliar (a) carbohydrates (mean ± S.E.M.), and (b) tannin (mean ± S.E.M.) concentrations over time in 1998 (○) and 1999 (■).

calcium (Fig. 2a, $F_{1,201} = 853.1$, $P < 0.001$), magnesium (Fig. 2b, $F_{1,201} = 1816.8$, $P < 0.001$), nitrogen (Fig. 2c, $F_{1,116} = 41.7$, $P < 0.001$), and potassium (Fig. 2e, $F_{1,119} = 367.1$, $P < 0.001$). Phosphorous was the only nutrient found in greater concentrations in 1998 (Fig. 2d, $F_{1,108} = 294.5$, $P < 0.001$). All nutrients varied within the season in both years (Fig. 2). Nitrogen, phosphorous, and potassium tended to decrease over time, calcium tended to increase, and magnesium levels remained somewhat constant. Burn treatment had no significant effect on foliar nutrients in either year (Table 1), but in 1998 foliar calcium was marginally higher in seedlings from non-burned sites, and lowest in seedlings from sites with single-year burns (LSD $F_{2,4} = 5.53$; $P = 0.056$).

Seedling root characteristics were largely unaffected by burning, but root length and root mass tended to be greater in seedlings sampled from burned sites (Table 2). Although root density was unaffected by site treatments in the year of the burn, 1 year post-burn root density was significantly greater in seedlings from twice-burned sites than in seedlings from non-burned controls (Table 2). Root carbohydrate concentrations were not affected by burn regime (Table 2), but were significantly greater in seedlings sampled in 1999 than in those sampled in 1998 ($F_{1,22} = 34.01$; $P < 0.0001$), with a marginally significant burn by year interaction ($F_{2,22} = 2.8$; $P < 0.08$).

Table 1
Components ((S.E.M.) (%) dry wt) of *Q. alba* seedling foliage in once-burned (1x), twice-burned (2x), and non-burned control sites in the Daniel Boone National Forest, eastern Kentucky (US) 1998 and 1999

| Foliar component	Year	Burn treatment			F_{df}/Pr> F
		1x	2x	Non-burned	
Carbohydrates	1998	4.29 (0.16)	3.77 (0.15)	4.19 (0.13)	$F_{2,29} = 0.74/0.49$
	1999	5.78 (0.18)	5.17 (0.15)	5.54 (0.22)	$F_{2,24} = 0.11/0.90$
Tannins	1998	0.14 (0.01)	0.15 (0.01)	0.14 (0.01)	$F_{2,8} = 0.60/0.57$
	1999	0.11 (0.01)	0.12 (0.01)	0.10 (0.01)	$F_{2,22} = 1.25/0.31$
Calcium	1998	0.59 (0.06)	0.66 (0.06)	0.80 (0.05)	$F_{2,4} = 5.53/0.06$
	1999	1.51 (0.17)	1.69 (0.18)	1.63 (0.15)	$F_{2,4} = 0.32/0.74$
Magnesium	1998	0.17 (0.01)	0.18 (0.01)	0.18 (0.01)	$F_{2,28} = 0.43/0.65$
	1999	0.35 (0.02)	0.36 (0.02)	0.38 (0.02)	$F_{2,3} = 2.31/0.22$
Nitrogen	1998	1.48 (0.10)	1.43 (0.11)	1.55 (0.09)	$F_{2,4} = 1.05/0.41$
	1999	1.92 (0.19)	1.89 (0.20)	1.89 (0.17)	$F_{2,88} = 0.02/0.98$
Phosphorous	1998	0.13 (0.01)	0.14 (0.01)	0.14 (0.01)	$F_{2,3} = 0.07/0.94$
	1999	0.10 (0.01)	0.11 (0.01)	0.12 (0.01)	$F_{2,3} = 1.84/0.28$
Potassium	1998	0.64 (0.04)	0.63 (0.04)	0.63 (0.03)	$F_{2,8} = 0.02/0.98$
	1999	1.06 (0.09)	1.05 (0.09)	1.13 (0.08)	$F_{2,7} = 0.30/0.75$
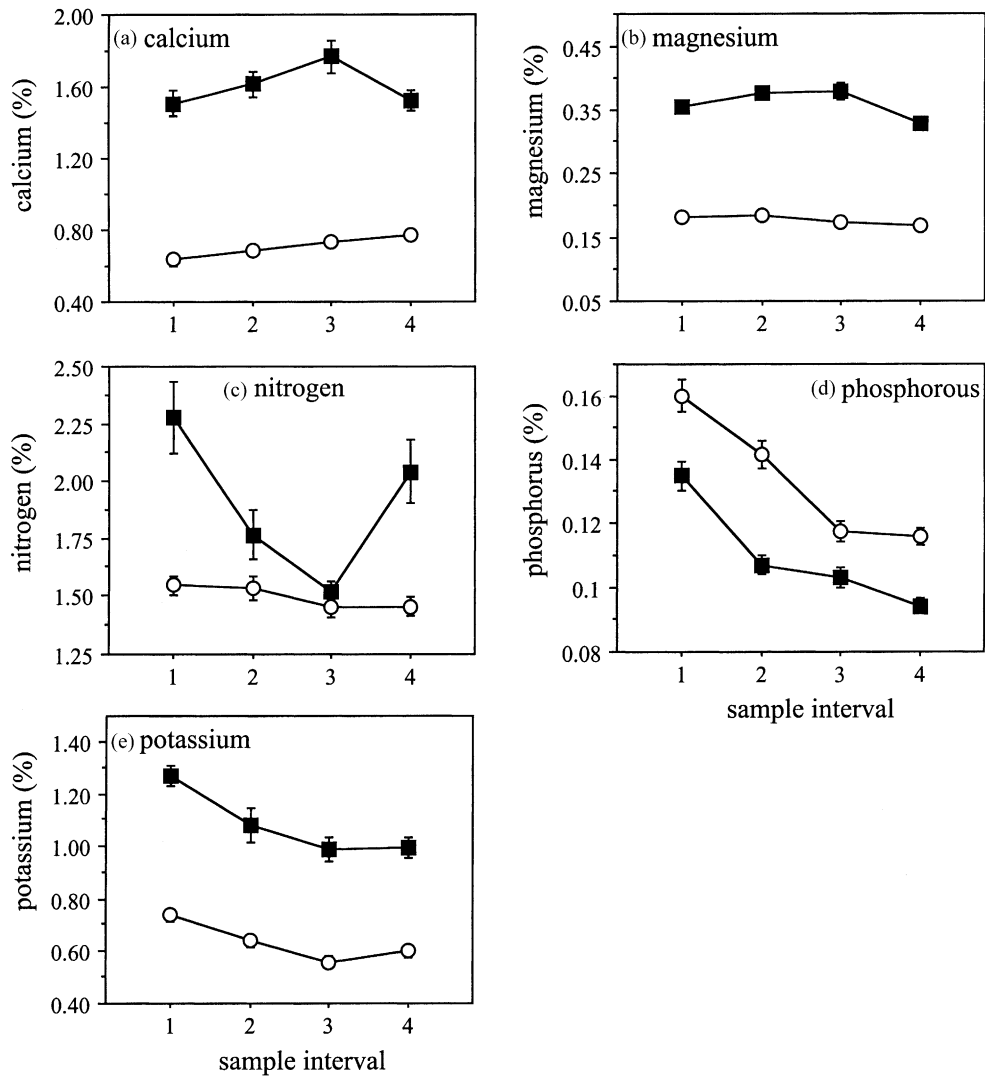
Fig. 2. *Q. alba* seedling foliar nutrient concentrations (mean ± S.E.M.) over time in 1998 (○) and 1999 (■).

3.2. Herbivore manipulation

Experimentally damaged white oak seedlings received equivalent levels of herbivory across site (burned versus non-burned) treatments (Fig. 3a, $F_{1,11} = 2.97$; $P = 0.11$). However, a moderately significant burn by time interaction ($F_{1,8} = 4.12$; $P = 0.07$) indicates that on 26 September, seedlings in burned plots received greater herbivore damage than those in non-burned plots ($|t|_{1,14} = 2.27$; $P = 0.04$). For both assay dates, levels of damage on herbivore-challenged seedlings were >40%, whereas levels on unchallenged seedlings were <5% (Fig. 4b, 1 May: $\chi^2 = 57.6$; $P = 0.0001$, and 26 September: $\chi^2 = 20.7$; $P = 0.0001$).

Foliar nitrogen levels were equivalent in seedlings from burned and non-burned sites, and tended to decrease over time independent of burn treatments (Fig. 3c; $F_{1,3} = 6.07$; $P = 0.09$). Foliar nitrogen was significantly lower in herbivore-challenged seedlings (Table 3), with a significant date by treatment interaction. For the 1 May assay, foliar nitrogen was higher in unchallenged seedlings (Fig. 3d; $|t|_{1,13} = 4.11$;

Table 2
Root characteristics (S.E.M.) of *Q. alba* seedlings collected from once-burned (1*x*), twice-burned (2*x*), and non-burned control sites in the Daniel Boone National Forest, eastern Kentucky (US) 1998 and 1999

Root characteristic	Year	Burn treatment			F_{df}/Pr> F
		1*x*	2*x*	Non-burned	
Length (cm)	1998	23.99 (1.91) a	22.58 (1.91) a	20.24 (1.48) a	$F_{2,30} = 1.29/0.28$
	1999	21.12 (1.67) a	18.97 (1.67) a	18.27 (1.67) a	$F_{2,6} = 0.79/0.49$
Mass (g)	1998	6.16 (1.80) a	5.54 (1.81) a	2.89 (1.40) a	$F_{2,29} = 1.38/0.27$
	1999	3.47 (0.85) a	3.11 (0.93) a	2.00 (0.85) a	$F_{2,3} = 1.35/0.37$
Density (g/cm)	1998	22.18 (3.99) a	17.93 (4.01) a	12.80 (3.10) a	$F_{2,29} = 1.20/0.31$
	1999	15.15 (2.96) ab	15.66 (3.28) a	10.79 (2.96) b	$F_{2,23} = 3.92/0.03$
Carbohydrates	1998	3.87 (0.53) a	4.16 (0.39) a	4.61 (0.48) a	$F_{2,21} = 0.63/0.54$
	1999	5.99 (0.49) a	5.72 (0.41) a	5.45 (0.29) a	$F_{2,21} = 0.44/0.65$

Means within rows followed by the same letter are not significantly different by LSD at $P = 0.05$.

Table 3
Foliar nitrogen, carbohydrate, and tannin (S.E.M.) concentrations of herbivore-challenged (caged with caterpillars) vs. unchallenged (caged without caterpillars) *Q. alba* seedlings in the Daniel Boone National Forest in southern Kentucky

Foliar component (%)	Seedling treatment		F_{df}/Pr> F
	+ Caterpillars	− Caterpillars	
Nitrogen	1.67 (0.15) b	1.90 (0.15) a	$F_{1,13} = 10.64/0.006$
Carbohydrates	5.91 (0.18) b	7.05 (0.18) a	$F_{1,17} = 26.04/0.0001$
Tannins	0.15 (0.02) a	0.17 (0.02) a	$F_{1,22} = 4.10/0.06$

Means within rows followed by the same letter are not significantly different (LSD).

$P = 0.001$), but there was no difference in nitrogen levels between herbivore-challenged and unchallenged seedlings in the 26 September assay.

Foliar carbohydrates increased over the growing season and were equivalent in seedlings from burned and non-burned sites across assay dates (Fig. 3e), regardless of whether or not seedlings were caged with caterpillars (Fig. 3f). However, foliar carbohydrates in herbivore-challenged seedlings were significantly lower than in unchallenged seedlings (Table 3 and Fig. 3f), and were significantly affected by assay date (Fig. 3f; $F_{1,10} = 78.42$; $P < 0.0001$).

Foliar tannins decreased over the growing season, and were equivalent in seedlings from burned and non-burned sites (Fig. 3g). Herbivore-challenged seedlings had marginally lower tannin concentrations than did those without herbivores (Table 3 and Fig. 3h), and tannin production decreased over the growing season on both herbivore-challenged and unchallenged seedlings (Fig. 3h; $F_{1,23} = 83.31$; $P < 0.0001$).

4. Discussion

Although levels of foliar nutrients and defense compounds can be influenced by environmental conditions (Kramer and Kozlowski, 1979; Mooney et al., 1991), we found relatively few fire-induced differences in white oak seedling phytochemistry. Our results vary from those found in other systems. For example, Reich et al. (1990), working in oak forests of the upper midwest (US), found concentrations of several foliar nutrients were enhanced by burning. Rieske (in press) found fire-induced changes in chestnut oak foliar carbohydrates, nitrogen, and tannins in response to a high-intensity fall wildfire. Similarly, studies in conifers by Christensen (1977) and Stark and Steele (1977) found burning altered foliar nutrient concentrations. It is possible that in our study foliar nutrients were impacted by burning in 1998, but that early-season differences in nutrient uptake disappeared before we sampled the fully expanded leaves
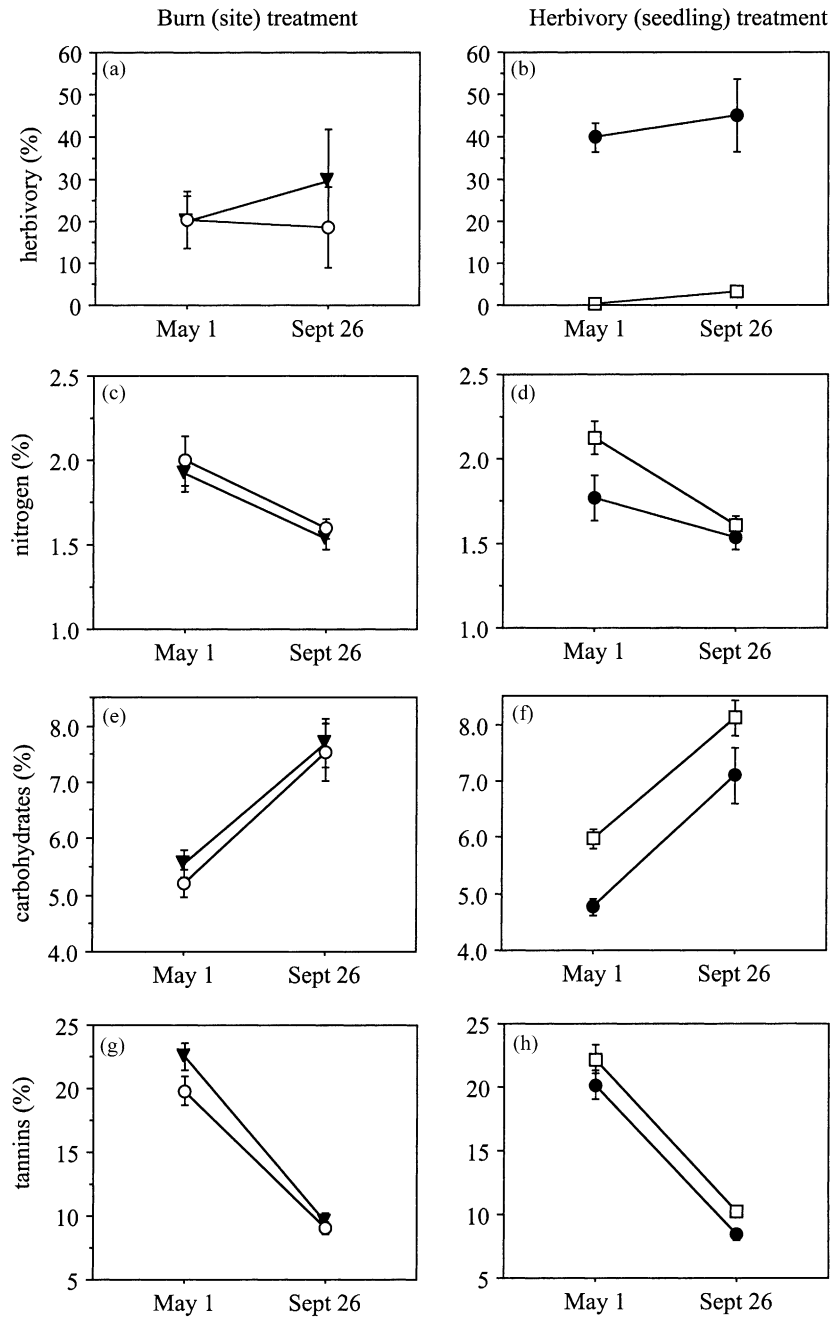
Fig. 3. Effects of burning (▼) vs. non-burning (○) (column 1), and herbivore-challenged (●) vs. unchallenged (□) (column 2), on *Q. alba* seedling (a) and (b) herbivory levels (mean ± S.E.M.), (c) and (d) foliar nitrogen, (e) and (f) carbohydrate, and (g) and (h) tannin concentrations over time in the Daniel Boone National Forest in southern Kentucky, 1999.

of the new oak sprouts following the fire (Reich et al., 1990). The absence of a measurable nutrient response may also have occurred because the nutrient load released by burning remained bound in the soil (DeBano et al., 1998), because our prescribed fires were too cool to adequately combust the organic layer, or because white oak seedling physiology is particularly non-responsive to low-intensity fire as a disturbance force.

Differences in phytochemical parameters were evident between years, with foliar carbohydrates and most nutrients higher 1 year post-burn, and foliar tannin levels higher in the burn year. Enhanced concentrations of foliar components in 1999 may have been a response to the extreme drought suffered in the region in 1999 (University of Kentucky, 1999), which inevitably impacted plant growth and metabolism.

Phytochemical differences within a season were apparent, independent of burn regime. In contrast to Feeny (1970), foliar tannin concentrations were greatest early in the season, declining as the season progressed. These finding are consistent with Wold and Marquis (1997), who also found seasonal declines in white oak foliar tannins in both herbivore-damaged and undamaged foliage. Similarly, Faeth (1985) found seasonal declines in hydrolyzable tannins in the evergreen emory oak. Foliar phenolic concentrations, including both hydrolyzable and condensed tannins, vary seasonally (Makkar et al., 1992) and are positively correlated with light penetration (Dudt and Shure, 1994), suggesting that white oak seedlings rely on tannins for defense against early-season herbivory, when sunlight penetration through the canopy is at a maximum. In our study foliar tannins remained elevated in seedlings from burned sites during the burn year (1998), perhaps due to increased light penetration, which supports this view. Given the imminence of canopy closure in deciduous forests, as well as the cost of tannin production, seedlings may rely on alternative defenses against late-season herbivory, such as increases in leaf toughness (Feeny, 1970; Choong, 1996).

Within years, the pattern of foliar carbohydrates and tannins appears inversely related, supporting views of plant carbon allocation which suggest that plants in resource-limited environs must opt for growth or defense (Bryant et al., 1993). Our results do not fully support the hypothesis that young, vigorously growing

plant tissues, such as those resulting from management regimes employing prescribed fire, are a higher quality food source and, therefore, more prone to herbivore attack than older, less metabolically active foliage (Price, 1991). Herbivore-induced declines in foliar quality may be alleviated in nutrient-rich, burned sites, as seedlings allocate resources to growth rather than defense, thereby enhancing plant and herbivore performance. The phenomenon of enhanced herbivore preference for and performance on juvenile plant tissue has been demonstrated (Whitham and Mopper, 1985; Price et al., 1987; Hunter and Schultz, 1995), and increased consumption by leaf-feeding caterpillars has been correlated with high carbohydrate, low phenolic foliage in other systems (Redak and Cates, 1984; Hartley and Lawton, 1987; Rieske and Raffa, 1998). The lepidopteran defoliators we used to challenge seedlings produced foliar damage approximately five times greater than were found endemically at these sites (Adams and Rieske, 2001), and are equivalent to or greater than herbivory levels produced in similar studies (Faeth, 1985; Hunter and Schultz, 1995; Wold and Marquis, 1997). Our results may be confounded, however, by variability between herbivore species and by additional abiotic factors influencing herbivore activity and plant physiological responses. We measured herbivore-induced phytochemical responses, and not plant growth or herbivore performance, in this study.

Results presented here suggest that early in the season white oak seedlings may chemically defend their foliage with high tannin levels, while low nitrogen concentrations, and possibly leaf toughness (Choong, 1996), act as anti-herbivore mechanisms late in the season. Although enhanced herbivory levels have been attributed to fire-induced phytochemical changes in some systems (Stein et al., 1992; Viera et al., 1996), selection of white oak seedlings as potential host plants by herbivores appears unaffected by the low intensity fires in this study. Given that herbivore consumption is often attributed to an optimal balance of nutrients (Mattson and Scriber, 1987; Clancy et al., 1993), late winter prescribed fire appears relatively unimportant in manipulating seedling phytochemistry and herbivore host selection in this system. Our results indicate that low intensity fire has minimal effects on the defensive abilities and palatability of white oak seedlings, and suggests that oak/ herbivore

relationships should not influence management decisions regarding the use of prescribed fire for enhancing regeneration of our oak forests.

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