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# Wildfire alters oak growth, foliar chemistry, and herbivory

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## Abstract

Fire is a major disturbance factor influencing the formation and maintenance of oak (*Quercus*)-dominated forests of eastern North America. Fire suppression practices have resulted in declining oak dominance, and caused the loss of oak seedlings due to poor light regimes and vegetative competition. Both wildfires and prescribed fires can alter forest stand composition and influence succession. Fire can also cause physiological changes in plants, potentially influencing growth, competition, and susceptibility to herbivory. Fire may impact herbivore populations directly by altering habitat and abundance, or indirectly through alterations in food supply. The objective of my study was to assess the effects of a naturally occurring wildfire on chestnut oak (*Q. prinus* L.) seedling growth, foliar chemistry, and suitability to a generalist herbivore, the gypsy moth (*Lymantria dispar* L.). I sampled chestnut oak seedlings four times for phytochemical analysis throughout the post-fire growing season, and sampled once to assess suitability for caterpillar performance and to measure seedling growth. Chestnut oak seedlings sampled from burned sites had significantly higher foliar nitrogen and water content than seedlings sampled from non-burned sites. Seedlings from burned sites had transient declines in foliar carbohydrate concentrations, and also had higher initial tannin levels. Although seedlings from burned sites were smaller with respect to stem diameter and height, they grew more with respect to absolute growth rate, leaf area, and biomass, than their non-burned counterparts. In spite of the differences in leaf chemistry, there were no significant differences in the growth or development of gypsy moth caterpillars fed foliage from burned versus non-burned seedlings.

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## 1. Introduction

Fire is a major factor influencing the formation and maintenance of oak (*Quercus*)-dominated forests of eastern North America. In addition to a suite of other disturbance factors, including herbivory, pathogens, human use, and climate change, fire has affected the development and dominance of oak forests throughout the region (Abrams, 1992). Historically, both naturally occurring and human-ignited intermittent fire was an essential component of the disturbance regime

influencing forest succession (Russell, 1983; Delcourt and Delcourt, 1998).

Both wildfires and prescribed fires modify vegetation physiology, altering photosynthetic rates and efficiency, thereby influencing competitive abilities and successional status (Reich et al., 1990; Kruger and Reich, 1997a). Physiological changes in post-fire leaf photosynthetic capacity may be caused by an increase in the root/shoot ratio due to reduced foliar biomass (Wareing et al., 1968), changes in foliar nutrient concentrations resulting from increases in soil nutrient availability (Oechel and Hastings, 1983), changes in leaf gas exchange (Kruger and Reich, 1997b), or a decrease in the source/sink ratio in post-burn vegetation

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(Neales and Incoll, 1968). These physiological changes in post-burn vegetation may lead to a decline in growth rates of oak competitors (Kruger and Reich, 1997c; Arthur et al., 1998), increases in oak seedling growth rates (Adams and Rieske, 2001), or altered growth of overstory trees (Boerner et al., 1988; Rieske et al., 2001). Foliar defensive chemistry also may be affected by increases in soil nutrients (Hunter and Schultz, 1995) or sunlight (Dudt and Shure, 1994). Given the potential changes in the nutritional and defensive composition of post-burn oak foliage, foliar suitability and susceptibility to herbivores may be altered.

The gypsy moth (*Lymantria dispar* L., Lepidoptera: Lymantriidae) is an introduced polyphagous herbivore capable of defoliating oak stands. The impact of gypsy moth outbreaks can include shifts in forest stand composition away from oak dominance (Campbell and Sloan, 1977; Gottschalk, 1993; Fajvan and Wood, 1996; Davidson et al., 1999), similar to shifts in stand composition due to fire suppression. Wildfires can promote oak regeneration, reverse the increasing prevalence of invasive plant species, and mitigate the effects of gypsy moth defoliation by enhancing stand vigor and manipulating species composition (Gottschalk, 1993). Wildfires may impact herbivore populations directly by altering habitat, abundance, and species composition (Siemann et al., 1997), or indirectly via alterations in food availability and quality. Indirect effects of fire on herbivory may result from changes in phytochemistry that impact herbivore success.

The Red River Gorge Geological Area of the Daniel Boone National Forest in eastern Kentucky, USA, was struck by a series of wildfires in November 1999, which were fed by the build-up of fuels due to fire suppression programs, and exacerbated by the extreme drought in the region in the summer of 1999 (Williams, 1999). The Red River Gorge is located in the Cumberland Plateau and is characterized by deeply dissected xeric ridge tops that support several species of oak, including chestnut (*Q. prinus* L.), scarlet (*Q. coccinea* Muenchh), white (*Q. alba* L.), and black (*Q. velutina* Lam.), several pine species, including pitch (*Pinus rigida* Mill.), shortleaf (*P. echinata* Mill.), and Virginia (*P. virginiana* Mill.), and red maple (*A. rubrum* L.) (Braun, 1950). My objective was to assess the effects of a naturally occurring wildfire on chestnut oak seedling growth, foliar chemistry, and suitability to an insect herbivore. I chose to examine

the effects of wildfire on chestnut oak because of its prevalence in the region (Braun, 1950) and its importance as a member of the oak component of eastern deciduous forests (Burns and Honkala, 1990).

## 2. Methods

### 2.1. Study sites and sampling

I established study plots on burned and non-burned sites ( $N = 3$ ) in early spring 2000. Because the area had been burned by wildfires, no specific information regarding fire characteristics were available. However, plots on burned sites were established in areas with similar characteristics with respect to slope, aspect, species composition, and apparent fire intensity (litter layer fully combusted, with mineral soil visible, scorch height averaging <2 m, scarring evident, fire mortality low). On each site, three plots of chestnut oak seedlings were located a minimum of 50 m apart. Fifty seedlings in each plot were flagged for destructive sampling throughout the growing season. Because chestnut oak re-sprouts in response to fire and other mortality factors, I defined a seedling as a small oak (generally <25 cm) appearing less than several years old from above-ground investigation. Plots on adjacent non-burned sites were similarly chosen as controls.

Seedlings were sampled for phytochemical analysis on 18 May, 5 June, 28 June, and 9 August 2000. At each interval, seedlings ( $N = 10$ ) from each plot were excised at the base, immediately placed in water in an ice cooler, and returned to the laboratory for processing. Thus, for each sample date, 10 seedlings were sampled from each of three plots on three burned sites, for a total of 90 seedlings from burned sites, and 90 seedlings from non-burned sites. On 5 June only, additional seedlings ( $N = 10$ ) were sampled from each plot for herbivore feeding trials.

### 2.2. Phytochemical analysis

Leaves from each seedling were removed at the base and divided into two groups; one group was flash frozen in liquid nitrogen for foliar chemical analysis, and the other was designated for fresh weight analysis. Foliage that was flash frozen was immediately ground

into a fine powder and stored at  $-80^{\circ}\text{C}$ . Tissue was then freeze-dried (VirTis Freezemobile 12SL, The VirTis Company Inc., Gradiner, NY) for approximately 36 h and stored at  $-80^{\circ}\text{C}$  prior to analysis of foliar total non-structural carbohydrates, tannins, and nitrogen. Foliar carbohydrate analysis was conducted spectrophotometrically with an anthrone/thiourea reagent (Quarmby and Allen, 1989). Foliar nitrogen was analyzed using a Leco 428 nitrogen determinator (Leco Corp., St. Joseph, MI). 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.

Leaves used for fresh weight analysis were excised at the leaf base, and leaf area (LI-3100 Area Meter, LI-COR Inc., Lincoln, NE) and fresh weight were measured. I determined foliar toughness by measuring the force (kg) necessary to penetrate fresh leaf tissue using a force gauge fitted with a pointed cone attachment (Mark 10 Corp., Hicksville, NY). After 6 days drying at  $60^{\circ}\text{C}$ , dry weight measurements were recorded, and foliar water content and specific leaf mass ( $\text{mg}/\text{cm}^2$ ) were calculated.

### 2.3. Seedling growth

In March 2001, I measured seedling growth from four of the six sites (two burned and two non-burned sites) to determine whether seedlings in burned areas had different size and rate of growth than those in unburned areas. To determine initial seedling height, I measured the length from a pre-determined basal stem mark to the tip of the previous year's terminal node. To determine final seedling height, I measured the length from the pre-determined basal stem mark to the tip of the leading branch. Because pre-burn measurements were not taken and initial seedling height in burned sites was zero, relative growth rates could not be determined. Therefore, I calculated the absolute growth rate of seedling height according to methods from Hunt (1990).

$$\frac{\text{final seedling height} - \text{initial seedling height}}{\text{time 2} - \text{time 1}}$$

where time 2 – time 1 was 1 year. I also measured basal stem diameter by averaging two perpendicular basal measurements at the pre-determined point near the root collar.

### 2.4. Herbivore feeding assays

Herbivore performance assays were conducted by allowing caterpillars to feed for the duration of the fourth stadium on chestnut oak from burned and non-burned plots, using leaves collected only from the 5 June 2000 sample date. Gypsy moth caterpillars (USDA-ARS Laboratory, Otis AFB MA, USA) were held in growth chambers with a 15:9 (L:D) photoperiod at  $23^{\circ}\text{C}$ , in the University of Kentucky Forest Entomology Quarantine facility. Newly molted caterpillars previously fed a wheat germ-based artificial diet (Southland Products Inc., Lake Village, AR, USA) were starved for 24 h prior to use in assays. Whole leaves were excised at the petiole, surface-sterilized in 0.1% sodium hypochlorite solution, individually weighed, and placed in florists' water picks in  $7\text{ cm} \times 21\text{ cm}$  clear plastic rearing boxes. One caterpillar ( $N = 20$  per treatment) was placed in each rearing box and monitored at 24 h intervals for the duration of the stadium. At 2–3 days intervals, leaves were obtained from the original seedlings, which were held in water picks in an ice chest, and replaced to ensure freshness. Immediately after molting, insects were removed from the foliage and frozen, and plant tissue, insect cadavers and waste material were oven dried at  $60^{\circ}\text{C}$  for 5 days and weighed. Relative growth rate ( $\text{RGR} = \text{caterpillar biomass gained (mg)}/\text{initial caterpillar dry wt. (mg)} \times \text{time (days)}$ ) and length of caterpillar stadium (duration of fourth instar in days) were calculated as measures of caterpillar performance and foliar suitability.

### 2.5. Statistical analysis

Data on foliar characteristics were analyzed using a repeated measures mixed model analysis of variance (Proc Mixed, SAS Institute, 1997), with site treatment (burn) and date as fixed effects, plot nested within treatment as a random effect, and plant foliar characteristics as response variables. Whereas most response variables were analyzed with an unstructured covariant structure, I used an autoregressive covariant structure for leaf area and dry weight, resulting in varying degrees of freedom (Littell et al., 1996). In addition, Satterthwaite's approximations were used to determine degrees of freedom, so results contain decimal degrees of freedom as calculated by SAS.

A least significant difference (LSD) procedure was used to analyze all pairwise comparisons. Because plant growth data were not normally distributed, plant growth was analyzed using the Mann–Whitney non-parametric rank test (Abacus Concepts, 1989), with seedling height, absolute growth rate, and basal stem diameter as dependent variables. Herbivore performance was analyzed using analysis of variance, with relative growth rate and length of caterpillar stadium as dependent variables, and site treatment (burn) as the independent variable. Because analyzing growth indices alone can lead to spurious conclusions, initial caterpillar weights were used as covariates in the analysis (Raubenheimer and Simpson, 1992). A LSD test was used to analyze differences in plant and herbivore growth.

### 3. Results

#### 3.1. Phytochemical analysis

Foliar carbohydrate levels were equivalent in chestnut oak seedlings from burned and non-burned plots across the growing season (Table 1). Sample date was a significant factor affecting foliar carbohydrates (Fig. 1A,  $F_{3,16} = 15.93$ ,  $P < 0.0001$ ), with levels in all seedlings generally increasing as the season progressed, but with a significant burn  $\times$  date interaction ( $F_{3,16} = 6.00$ ,  $P = 0.0061$ ). Early season carbohydrate levels were marginally greater in foliage from non-burned seedlings on 18 May ( $|t|_{1,11} = 1.83$ ,  $P = 0.0950$ ), and significantly greater in non-burned foliage on 5 June ( $|t|_{1,11.8} = 2.97$ ,  $P = 0.0119$ ), but there were no differences in foliar carbohydrates

between burned and non-burned seedlings as the season progressed (Fig. 1A).

Levels of foliar nitrogen were significantly greater in seedlings from burned plots than in seedlings from non-burned plots (Table 1). Foliar nitrogen concentration was also significantly impacted by sample date, progressively declining in both burned and non-burned seedlings (Fig. 1B,  $F_{3,16} = 43.11$ ,  $P < 0.0001$ ). Seedlings from burned plots had significantly greater foliar nitrogen levels on 18 May ( $|t|_{1,16} = 3.10$ ,  $P = 0.0069$ ), 28 June ( $|t|_{1,16} = 3.22$ ,  $P = 0.0054$ ), and 9 August ( $|t|_{1,16} = 2.69$ ,  $P = 0.0162$ ). Only on 5 June there was no significant difference in foliar nitrogen levels in seedlings from burned versus non-burned plots (Fig. 1B).

Foliar tannin levels, as measured by protein binding capacity, were not affected by burning across sample dates (Table 1). However, there was a significant date effect ( $F_{3,16} = 44.45$ ,  $P < 0.0001$ ), as well as a significant burn  $\times$  date interaction ( $F_{3,16} = 5.89$ ,  $P = 0.0066$ ). Early in the season (18 May), tannin levels in foliage from burned seedlings were greater than tannin levels in foliage from non-burned seedlings (Fig. 1C,  $|t|_{1,16} = 2.65$ ,  $P = 0.0175$ ). Foliar tannins declined by 5 June, and were not significantly different in burned and non-burned seedlings. On 28 June, tannin levels increased and were significantly greater in seedlings from non-burned sites ( $|t|_{1,16} = 3.54$ ,  $P = 0.0027$ ), but by 9 August these differences were no longer significant (Fig. 1C).

Specific leaf mass was not affected by burning across sample dates (Table 1). Specific leaf mass varied with sample date ( $F_{3,16} = 38.61$ ,  $P < 0.0001$ ), increasing seasonally (Fig. 1D), and with a significant burn  $\times$  date interaction ( $F_{3,16} = 6.38$ ,  $P < 0.0048$ ).

Table 1

Foliar characteristics of chestnut oak seedlings (mean  $\pm$  S.E.) sampled on four dates in 2000 from sites in the Daniel Boone National Forest, eastern Kentucky, USA, burned by a fall 1999 wildfire

Foliar characteristic	Site treatment		$F_{d.f.}/P > F$
	Burned	Non-burned	
Carbohydrates (dry wt.%)	5.85 (0.09)	6.07 (0.08)	$F_{1,15.1} = 2.33/0.15$
Nitrogen (dry wt.%)	2.16 (0.05)	1.99 (0.03)	$F_{1,16} = 12.53/<0.01$
Tannins (protein ppt)	1.18 (0.04)	1.17 (0.03)	$F_{1,16} = 0.01/0.97$
Specific leaf mass (mg/cm <sup>2</sup> )	3.77 (0.12)	3.74 (0.10)	$F_{1,15.8} = 0.03/0.87$
Toughness (kg)	0.02 (0.0002)	0.01 (0.0003)	$F_{1,14.3} = 1.36/0.26$
Water content (mg)	2.75 (0.30)	1.50 (0.22)	$F_{1,13.7} = 35.79/<0.01$

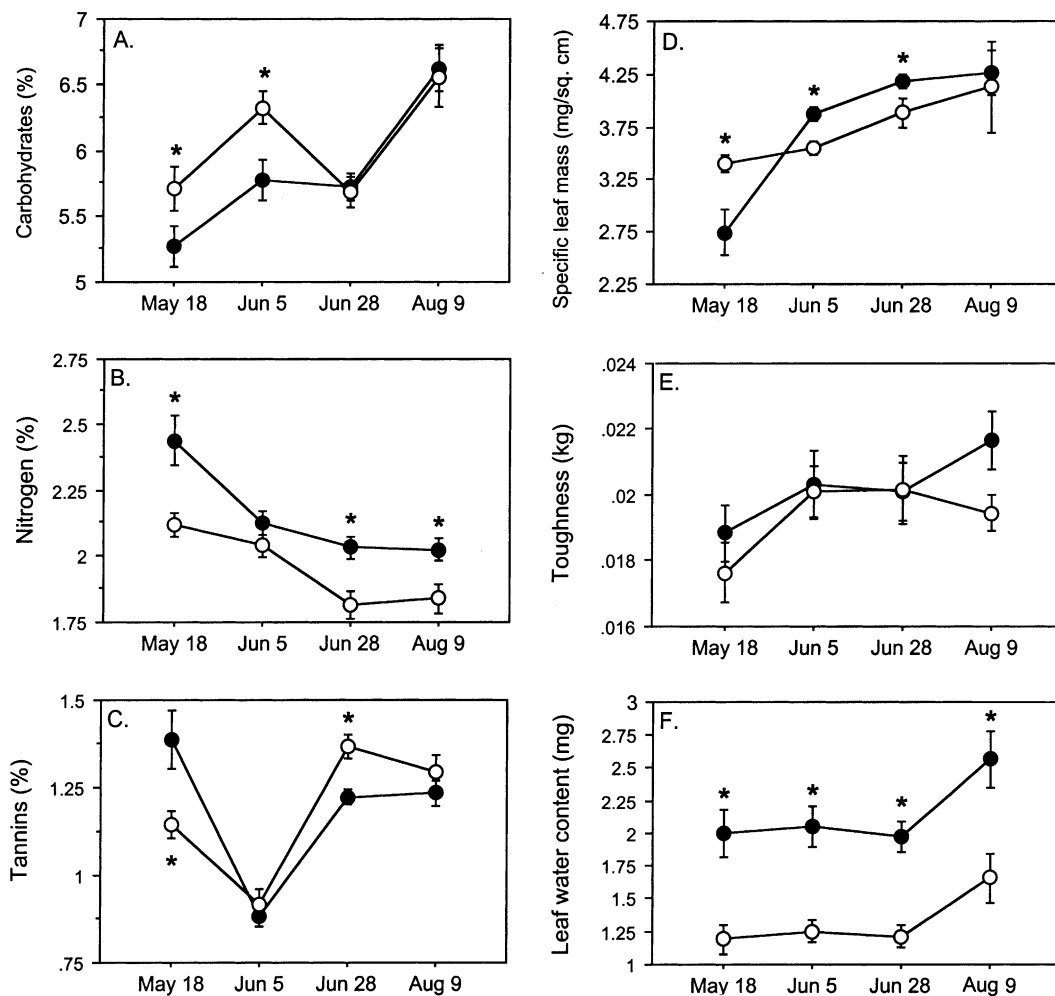


Fig. 1. Seasonal phytochemical and physical characteristics of chestnut oak seedlings sampled in 2000 from sites in the Daniel Boone National Forest (eastern Kentucky, USA) which had experienced a fall 1999 wildfire. Burned (●) and non-burned (○) sites. A: foliar carbohydrates; B: nitrogen; C: tannins; D: specific leaf mass; E: toughness; F: leaf water content. Asterisk (\*) denotes significant difference (see text for statistical values).

On 18 May, specific leaf mass was significantly greater in non-burned foliage than burned foliage ( $|t|_{1,15.6} = 2.84$ ,  $P = 0.0121$ ). By 5 June this was reversed, and specific leaf mass of non-burned foliage was less than that of burned foliage ( $|t|_{1,15} = 4.17$ ,  $P = 0.0008$ ). This pattern continued as the season progressed, with specific leaf mass in non-burned foliage significantly less than that of burned foliage on 28 June ( $|t|_{1,14.8} = 2.20$ ,  $P = 0.0441$ ), but by 9 August the difference was no longer significant.

Foliar toughness was not impacted by burning (Table 1), but generally increased as the season

progressed in both burned and non-burned plots (Fig. 1E,  $F_{3,16} = 8.13$ ,  $P < 0.0016$ ).

Leaf water content was significantly impacted by burning (Table 1), with seedlings from burned plots containing higher leaf water content than seedlings from non-burned plots across all dates. Date affected leaf water content (Fig. 1F,  $F_{3,16} = 5.72$ ,  $P < 0.0072$ ), which increased seasonally and was greater in seedlings from burned plots at every sample interval (18 May:  $|t|_{1,15.8} = 3.94$ ,  $P = 0.0012$ , 5 June:  $|t|_{1,15.4} = 4.71$ ,  $P = 0.0003$ , 28 June:  $|t|_{1,14.2} = 6.29$ ,  $P < 0.0001$ , 9 August:  $|t|_{1,13.3} = 3.65$ ,  $P = 0.0028$ ).

Table 2

Productivity of chestnut oak seedlings (mean  $\pm$  S.E.) in the Daniel Boone National Forest, eastern Kentucky, USA, burned by a fall 1999 wildfire, 1 year post-fire

Seedling parameter	Site treatment		Test statistic/probability
	Burned	Non-burned	
Basal stem diameter (cm)	2.68 (0.08)	4.15 (0.15)	$ Z _{1.d.f.} = 7.39/0.0001$
Initial seedling height (cm)	0 (0)	18.60 (0.81)	$ Z _{1.d.f.} = 9.45/0.0001$
Final seedling height (cm)	13.05 (0.55)	21.51 (0.83)	$ Z _{1.d.f.} = 7.23/0.0001$
Absolute growth rate (height in cm)	12.95 (0.56)	2.92 (0.18)	$ Z _{1.d.f.} = 9.39/0.0001$
Leaf area (cm <sup>2</sup> )	385.32 (0.74)	231.32 (3.88)	$F_{1,28.2} = 12.36/<0.002$
Leaf mass (g dry wt.)	1.57 (0.09)	0.80 (0.07)	$F_{1,23.2} = 29.42/<0.001$

Table 3

Performance of fourth instar gypsy moth caterpillars (mean  $\pm$  S.E.) fed foliage from chestnut oak seedlings collected from burned and non-burned sites in the Daniel Boone National Forest, eastern Kentucky, USA, 5 June 2000

	Site treatment		$F_{1,39}/P < F$
	Burned	Non-burned	
Relative growth rate	0.036 (0.007) a	0.047 (0.015) a	0.56/0.47
Stadium length (days)	10.52 (0.53) a	11.23 (0.38) a	1.50/0.22

### 3.2. Seedling growth

Seedlings from non-burned control plots were larger than those from burned plots with respect to basal stem diameter, initial height, and final height (Table 2). Pre-burn measurements were not taken, however, and relative growth rates cannot be calculated on seedlings with an initial height of zero. However, the absolute height growth of chestnut oak seedlings from burned sites was over four times greater than those from non-burned sites. Seedlings on burned sites grew nearly 13 cm in the year following the wildfire, whereas those in non-burned sites grew less than 3 cm (Table 2). Seedlings from burned plots were also more productive with respect to leaf area and leaf mass (Table 2).

### 3.3. Herbivore feeding assay

Herbivore performance was unaffected by the burn treatments (Table 3). Caterpillars fed foliage from chestnut oak seedlings sampled from burned plots had the same rate of relative growth ( $P = 0.47$ ) and development time ( $P = 0.22$ ) as did caterpillars fed foliage of seedlings from non-burned plots.

## 4. Discussion

The fall 1999 wildfires that swept through the Red River Gorge caused significant changes in the growth and foliar chemistry of chestnut oak seedlings the following growing season. Seedlings sampled from burned sites had higher levels of foliar nitrogen and higher water content compared to non-burned control seedlings. Differences in foliar carbohydrates and tannins were transient, but the enhanced nitrogen and leaf water levels in burned foliage remained for the duration of the growing season.

My data on chestnut oak leaf chemistry differs somewhat from studies in similar systems. Whereas I found a transient decrease in foliar carbohydrates in seedlings from burned sites relative to non-burned sites early in the season, Kruger and Reich (1997c) found the opposite in northern red oak seedlings, with a transient elevation in foliar carbohydrates following an early spring, low intensity surface fire. The increase in chestnut oak foliar nitrogen in my study is similar to results from Reich et al. (1990) and Kruger and Reich (1997c), who found enhanced, though transient, leaf nitrogen levels in northern red oak. The transient nature of the elevated nitrogen levels may be due to the

nature of the fire, which in the above studies was of lower intensity. Although it is possible that northern red oak seedlings respond differently to fire than chestnut oak seedlings, the difference in seedling response may be attributed to the timing (spring versus fall) and/or intensity (cool versus hot) of a prescribed burn, which may only partially combust the litter layer, versus a wildfire, which may fully combust the litter layer, exposing mineral soil. Wildfires tend to occur during the dry season, burning hotter and less uniformly than controlled, low intensity surface fires (Whelan, 1995). Stark and Steele (1977) demonstrated that hotter fires can lead to nutrient differences in post-burn vegetation for up to 3 years.

There was a significant burn  $\times$  date interaction with respect to foliar tannins and specific leaf mass. Initially, levels of foliar defensive tannins were higher in foliage from burned sites. Tannin levels declined in seedlings from both burned and non-burned sites on 5 June, but by the third sampling date the early trend was reversed and foliar tannins were significantly greater in foliage sampled from non-burned seedlings. Tannin production is proportionate to light penetration (Dudt and Shure, 1994), and may be related to nutrient availability (Hunter and Schultz, 1995), both of which were highest early in the season following the fire, and prior to canopy leaf-out. The initially high tannin production may be a response to the increase in light availability and soil nutrients caused by burning, which expends itself and gradually declines as the season progresses. By season's end there was no difference in foliar tannin concentrations in seedlings from burned versus non-burned sites.

Specific leaf mass was initially lower in foliage from burned sites, suggesting thinner leaves on these seedlings early in the growing season. Again, these differences were transient and by season's end there were no differences in specific leaf mass between the two site treatments.

The differences in size and growth of seedlings was expected, since the wildfire effectively burned seedlings to the surface. Besides an obvious and immediate impact on plant size, fire causes changes in soil nutrient availability (Prieto-Fernandez et al., 1993; Blankenship and Arthur, 1999), root/shoot ratios (Wareing et al., 1968), foliar nutrient concentrations (Oechel and Hastings, 1983), rates of leaf gas exchange (Kruger and Reich, 1997b), and source/sink

ratios (Neales and Incoll, 1968), all of which can lead to changes in post-burn seedling growth rates (Reich et al., 1990; Kruger and Reich, 1997c; Arthur et al., 1998; Adams and Rieske, 2001). Productivity of burned chestnut oak seedlings far exceeded their non-burned counterparts with respect to absolute growth rate and biomass (leaf area and leaf mass). While the differences in chestnut oak absolute growth rates on burned versus non-burned sites were striking, I would expect differences in the relative growth rates to be somewhat more moderate.

Gypsy moth caterpillar performance is influenced by leaf phenology (Schultz and Baldwin, 1982), which in turn affects foliar nitrogen (Lindroth et al., 1990), carbohydrates (Rieske and Raffa, 1998), and tannins (Schultz and Lechowicz, 1986). I found no significant difference in caterpillar performance, although caterpillars grew larger on chestnut oak foliage from non-burned sites and developed more rapidly on seedlings collected from burned sites (Table 3). Some of the plant characteristics that would be expected to enhance caterpillar performance (elevated nitrogen and thinner leaves with higher water content) were apparently not sufficiently high in this study to increase foliar palatability and accelerate caterpillar growth. The gypsy moth is a voracious herbivore, and may not be discriminating enough to be affected by subtleties in leaf chemistry caused by burning in the chestnut oak system. My results do not support current hypotheses regarding herbivore–plant relations, which predict that herbivore performance is enhanced on young, vigorously growing plant tissues (Price, 1991; Vieira et al., 1996), nor do my results support anecdotal evidence that post-burn re-growth in forest systems suffers higher herbivore pressure.

This study demonstrates that catastrophic, autumn wildfires alter chestnut oak foliar chemistry and enhance seedling growth, but may not alter the palatability of post-burn tissue to a generalist herbivore. Although the herbivore performance data were generated from only one sample date, these results suggest that fire-induced alterations in foliar palatability may not necessarily promote grazing by all herbivore guilds, and that catastrophic disturbances such as wildfires may act somewhat independently from other disturbance factors in influencing the establishment and maintenance of oak dominance in eastern forests.

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