

## Effects of prescribed fire on canopy foliar chemistry and suitability for an insect herbivore

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### Abstract

We assessed the effects of a prescribed fire on the phytochemical characteristics and vigor of overstory chestnut oak, scarlet oak, and red maple, and measured the impact of potential changes on herbivore fitness. We compared foliar carbohydrates, tannins, nutrients, and fiber concentrations in foliage from burned and non-burned forest canopies. There were significant differences in most foliar characteristics between tree species. Total non-structural carbohydrate concentrations in scarlet oak and red maple foliage, and calcium levels in red maple foliage, were significantly lower in burned plots, but other phytochemical characteristics were largely unaffected by burning. Tree growth also varied with species. Burning increased chestnut oak relative growth, decreased scarlet oak growth, and had no effect on red maple growth. Scarlet oak and red maple foliage from burned and non-burned forest canopies were assayed for gypsy moth performance. Caterpillars fed foliage from scarlet oak, the preferred host, grew larger and developed more rapidly than did those fed red maple foliage. There were no significant burn treatment differences in caterpillar development within either tree species, suggesting that managers using prescribed fire to promote oak regeneration need not worry about enhancing forest stand susceptibility to gypsy moth. However, the fire in this study was of low to moderate intensity; more intense fires may alter foliar palatability. © 2002 Elsevier Science B.V. All rights reserved.

**Keywords:** Oak; *Quercus*; Red maple; Phytochemistry; Gypsy moth; Defoliation

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### 1. Introduction

Since the implementation of effective fire suppression in the early to mid-1900s, forest stand composition in eastern North America has shifted to include greater dominance by shade tolerant species, and age and species mosaics have declined (Delcourt and Delcourt, 1998). As a result, seedlings in oak (*Quercus* spp.) dominated forests have become suppressed by

poor light regimes and vegetative competition from more aggressive, invasive species such as red maple (*Acer rubrum* L.) (Abrams, 1992). Lack of oak regeneration also has significant ecological consequences, including impacts on subsequent forest successional stages, and shifts in wildlife composition and distribution. The shift in species composition away from oak dominance in eastern deciduous forests has resulted in the decline of an extremely valuable hardwood group. Repeated attempts to reduce the decline of oaks and improve regeneration suggest that fire suppression is an important causal factor (Gammon et al., 1960; Beck and Hooper, 1986; Lorimer, 1989). Fire

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can reduce competition and increase sunlight, allowing oaks to thrive (Carvell and Tyron, 1961; Gottschalk, 1985; Muick and Bartolome, 1987). Competitors may effectively resprout after a single fire, but many oak competitors, including red maple, are successfully suppressed by repeated burning (Lorimer, 1985; Arthur et al., 1998). As a result of these potential benefits of prescribed burning on oak regeneration, prescribed fire is being used by managers, with potential consequences for the overstory oak.

Effects of fire on overstory oaks may include impacts on plant vigor, alterations in susceptibility to mortality agents, and fire damage to residual stems. Fire may influence plant growth and foliar chemistry by increasing nutrient concentrations in the soil (Prieto-Fernandez et al., 1993; Blankenship and Arthur, 1999). A transitory increase in foliar nitrogen, potassium, and phosphorus in tree seedlings has been observed directly following prescribed fire in some systems (Reich et al., 1990), which could be due to a post-fire increase in available soil nutrients, and which may manifest itself as increased seedling growth rates (Adams and Rieske, 2001), or increased growth of overstory trees (Boerner et al., 1988). Defensive phenolic compounds may also be affected by the increase in soil nutrients (Hunter and Schultz, 1995) or increased sunlight (Dudt and Shure, 1994). Given the potential effects of fire on oak phytochemistry, foliar nutritional suitability and susceptibility to mammalian and arthropod herbivores may be drastically altered.

The gypsy moth (*Lymantria dispar* L., Lepidoptera: Lymantriidae) is an introduced defoliator with outbreak potential that has become established throughout the northeastern US. The successful expansion of the geographic range of the gypsy moth into the central hardwood forests of the Appalachian Cumberland Plateau is assured by an abundance of several oak species, which are the insects' preferred host plants (USDA Forest Service, 1991; Leibhold et al., 1995). The impacts of gypsy moth outbreaks can be devastating, and 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.

Natural resource managers are increasingly turning to silvicultural techniques to mitigate the effects of

defoliation by the gypsy moth (Gottschalk, 1993). Selective harvesting, high-grading, and prescribed burning are potential methods to enhance stand vigor and manipulate forest species composition, thereby decreasing stand susceptibility to this and other invasive arthropod and plant species. Fire may impact herbivore populations directly by altering habitat, abundance, and species composition (Siemann et al., 1997), or indirectly via cascading effects caused by alterations in food quality and availability. Indirect effects of fire on herbivory may manifest themselves through changes in foliar characteristics that impact herbivore success. For example, fire may elicit accumulation of foliar nutrients, resulting in enhanced nutritional substrate that could ameliorate induced plant defenses (Haukioja et al., 1990). Fire may also cause plants to direct additional resources to growth processes, maintaining productivity but reducing defensive abilities (Price, 1991; Hunter and Schultz, 1995). Conversely, fire may deplete foliar nutrients and enhance production of defensive compounds. This is particularly relevant to the gypsy moth, which is responsive to enhanced nutritional substrate (Roth et al., 1994; Rieske and Raffa, 1998) and alterations in defensive phenolic compounds (Baldwin and Schultz, 1983; Schultz, 1988).

Regeneration of oak stands and suppression of invasive native and non-native plants and animals are emerging issues in deciduous forest management. The objectives of our study were to characterize the effects of fire on foliar chemistry of canopy oaks and red maple, to determine the effects of any fire-induced phytochemical changes on preferred and non-preferred host suitability to an insect folivore, and to assess how these potential changes may impact deciduous forest composition.

## 2. Methods

We assessed the impacts of a prescribed burn on the foliar chemistry and vigor of canopy chestnut oak (*Q. prinus* L.), and scarlet oak (*Q. coccinea* Muenchh.), both preferred hosts of the gypsy moth, and red maple, a non-preferred gypsy moth host. We also assessed the suitability of the burned and non-burned scarlet oak and red maple foliage for the development of gypsy moth caterpillars.

### 2.1. Study sites and sampling

This study was conducted in the Red River Gorge Geological Area of the Daniel Boone National Forest in eastern Kentucky (USA), in conjunction with the prescribed burn management program implemented by the US Forest Service. The Red River Gorge is located in the Cliff Section of the Cumberland Plateau and is characterized by xeric ridge tops supporting a diverse suite of oaks, including scarlet oak, chestnut oak, white oak (*Q. alba* L.), and black oak (*Q. velutina* Lam.), several species of pines (*Pinus rigida* Mill., *P. echinata* Mill., and *P. virginiana* Mill.), red maple, and mesic coves of beech (*Fagus grandifolia* Ehrh.), *Magnolia* spp., *Rhododendron* spp., and hemlock (*Tsuga canadensis* L.) (Braun, 1950).

Our experiment was conducted on a single ridge top. Four blocks were randomly located on the ridge, each of which were divided into two 20 × 20 m<sup>2</sup> plots. Prescribed fire was ignited across the entire ridge; one plot in each block was excluded from the fire with fire lines. Each non-burned plot had an additional 5 m wide non-burned buffer to minimize edge effects. Thus each of the four sections contained a burned area paired with a non-burned control.

Fires were started with a drip torch by firing a line from the highest point and the ridges first, and pulling strips downslope into the wind from the ridges. Point-source and strip firing were used to increase intensity to acceptable levels if backing and flanking fires were not of sufficient intensity (>0.3 m flame length). At the time of the prescribed fire on 2 April 1998, wind speed was 1–3 km/h, relative humidity was 36–42%, and air temperature was 9–10.5°C. The fire was a cool surface burn, with flame lengths of 30–90 cm which consumed primarily the previous year's leaf litter (D. Richardson, pers. comm.).

Individual trees selected for sampling were healthy and at least 5 m from any burned/non-burned interface; most were located more than 10 m from this interface. Canopy chestnut oaks had an average diameter (dbh) of 27.6 cm, scarlet oaks averaged 35.9 cm dbh, and the red maple, which were smaller co-dominants, averaged 16.0 cm dbh.

Foliar samples were obtained from two trees of each species in each plot by treatment combination ( $N = 48$ ). Foliage was sampled from the south side of the middle third of the canopy using a 12 gauge

shotgun to remove terminal branches on 6 May 1998, corresponding to leaf-out, and on 20 and 28 May, 3 and 17 June. On the first, second, fourth, and fifth sample dates, foliage was designated for phytochemical analysis, including foliar non-structural carbohydrates, tannins, nutrients, and fiber. On the third (28 May) sample date only, a smaller set of foliar samples ( $N = 16$ ) from scarlet oak and red maple were dedicated to gypsy moth feeding trials.

### 2.2. Phytochemical analysis

Leaves from each branch were removed at the base and divided into two groups; one was flash frozen in liquid nitrogen for analysis of carbohydrates and tannins, and the other was oven dried for nutrient and fiber analysis. Foliage that was flash frozen was immediately ground into a fine powder using a mortar and pestle, returned to the laboratory and stored at –80°C. Tissue was then freeze-dried (VirTis Freezemobile 12SL, The VirTis, Gradiner, NY) for approximately 36 h and stored at –80°C prior to analysis of foliar total non-structural carbohydrates and foliar tannins. Foliar carbohydrate analysis was conducted spectrophotometrically 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.

Leaves used for nutrient analysis were excised at the leaf base, packed in wet paper towels, stored on ice, and returned to the laboratory. Foliar leaf area (LI-3100 Area Meter, LI-COR, Lincoln, NE) and fresh weight were immediately measured. After a minimum of 6 days drying at 60°C, dry weight measurements were recorded and leaf area ratio (cm<sup>2</sup>/g dry wt) was calculated. Leaves were then ground to a fine powder and stored in a desiccator prior to nutrient analysis. Foliar nutrient concentrations were assessed using a block digestion method described by Isaac and Johnson (1976). Foliar acid-digested fiber (ADF) analysis was conducted by the University of Wisconsin Soil and Plant Analysis Laboratory (Madison, WI).

### 2.3. Tree growth

Using an increment borer, we sampled the radial growth of each of the 48 sample trees ( $N = 16$  per

species) in September 2000. To estimate basal area growth since 1998, the year of the burn, we estimated the basal area increment for each tree using diameter at breast height (dbh) and the sum of the last three years of radial growth. To determine whether trees on burned areas had different rates of growth than those on unburned areas, we calculated the relative growth rate of basal area since burning ( $\text{cm cm}^{-1} \text{time}^{-1}$ ) as follows (Hunt, 1990):

$$\frac{\ln(\text{final basal area}) - \ln(\text{initial basal area})}{\text{time 2} - \text{time 1}},$$

where final basal area was the basal area of the tree in 2000, initial basal area was the basal area of the tree in 1997, and time 2 – time 1 was 3 years.

#### 2.4. Insect assays

Gypsy moth performance assays were conducted on scarlet oak and red maple from burned and non-burned plots using leaves collected only from the 28 May 1998 sample date. Gypsy moth egg masses were obtained from the USDA-ARS laboratory (Otis AFB, MA, USA) and were surface sterilized with a 0.1% sodium hypochlorite solution. Prior to use in assays, larvae were reared on wheat germ based artificial diet (Southland Products, Lake Village, AR) in growth chambers with a 15:9 (L:D) photoperiod at 23°C. Newly molted third instar caterpillars were chosen at random from each of the 15 different egg masses. Caterpillars were starved for 24 h prior to use.

Caterpillar performance was assessed by allowing third instar larvae to feed for the duration of the stadium. Whole leaves were weighed and placed in florists' water picks in 7 cm × 21 cm clear plastic rearing boxes. One-third instar caterpillar was placed in each rearing box and monitored at 24 h intervals for the duration of the stadium. At each monitoring interval, larvae were weighed, and at 2–3 day interval leaves were replaced to ensure freshness. Five insects were used for each of the eight trees of both scarlet oak and red maple, for a total of 80 assays. At the completion of the assay, plant tissue, insect cadavers and waste material were oven dried at 60°C for a minimum of 10 days and weighed. Relative growth rate ( $\text{RGR} = [\text{caterpillar biomass gained (mg)}] / [(\text{initial caterpillar dry wt (mg)})(\text{time (day)})]$ ) and

length of caterpillar stadium (duration of third instar in days) were calculated as measures of insect performance.

#### 2.5. Statistical analysis

Data for foliar chemistry and insect assays were analyzed using analysis of variance (PROC MIXED; SAS Institute, 1997) on four blocks. We analyzed the dependent variables describing foliar characteristics (carbohydrate, tannin, nutrient, and fiber concentrations) across all three tree species before analyzing each tree species separately for burn effects. All pairwise comparisons were made using a least significant difference (LSD) test. Tree growth data were analyzed using a two-way ANOVA with species and treatment as the main effects. A significant interaction term ( $P = 0.01$ ) led to one-way ANOVA on each species separately. Caterpillar RGR and stadium length also were analyzed for species differences using ANOVA before analyzing for burn effects within species. All significant differences in caterpillar performance were assessed using Fisher's protected LSD.

### 3. Results

#### 3.1. Phytochemical analysis

*Foliar non-structural carbohydrates.* The three tree species differed significantly in foliar total non-structural carbohydrate concentrations (Table 1;  $F = 333.30$ ,  $P < 0.0001$ ), with levels in chestnut oak the highest and levels in red maple the lowest. Overall, foliar total non-structural carbohydrate levels were significantly lower in foliage from burned trees than foliage from non-burned trees across all three species ( $F = 4.67$ ,  $P = 0.0473$ ), with a strongly significant block effect ( $F = 6.40$ ,  $P = 0.0053$ ). Foliar carbohydrate concentrations also were affected by sample date across all species ( $F = 6.24$ ,  $P = 0.0009$ ).

Chestnut oak foliar total non-structural carbohydrate concentrations did not vary with burn treatment (Table 2) or date. Foliar carbohydrate levels were relatively high early in the season (Fig. 1A), declining during the second and third sampling intervals, and gradually increasing in the final interval.

Table 1

Characteristics (mean (S.E.)) of canopy chestnut oak, scarlet oak, and red maple across site treatments (burned and non-burned) on four sample dates in the Daniel Boone National Forest, Kentucky, 1998<sup>a</sup>

Foliar component	Species		
	Chestnut oak	Scarlet oak	Red maple
Carbohydrates (% dry wt)	2.49 (0.07) a	2.09 (0.06) b	0.94 (0.05) c
Tannins (% dry wt)	0.14 (0.01) b	0.34 (0.01) a	0.11 (0.01) c
Calcium (mg/g dry wt)	4.81 (0.19) a	3.47 (0.10) c	4.19 (0.15) b
Magnesium (mg/g dry wt)	1.80 (0.04) a	1.30 (0.02) b	1.35 (0.03) b
Nitrogen (mg/g dry wt)	24.48 (0.99) a	16.91 (0.75) b	19.46 (0.85) b
Phosphorous (mg/g dry wt)	2.37 (0.14) a	1.70 (0.08) b	1.66 (0.08) b
Fiber (acid-digested, % dry wt)	35.67 (0.98) a	25.29 (0.62) b	27.17 (1.19) b
Leaf area ratio (cm <sup>2</sup> /g dry wt)	203.53 (6.49) a	167.92 (5.18) b	214.65 (6.98) a
Relative basal area growth rate (cm <sup>2</sup> /cm <sup>2</sup> yr)	0.02 (0.002) b	0.02 (0.002) b	0.03 (0.002) a

<sup>a</sup> Means within rows followed by the same letter are not significantly different.

Scarlet oak foliage from trees on burned plots contained marginally lower levels of carbohydrates than did foliage on trees in non-burned plots across all dates (Table 2;  $F = 5.36$ ,  $P = 0.1035$ ). Carbohydrates in scarlet oak foliage were marginally affected by sample date ( $F = 2.89$ ,  $P = 0.0639$ ), with a strong date  $\times$  burn interaction ( $F = 5.41$ ,  $P = 0.0079$ ). Initial carbohydrate levels were slightly greater in burned than non-burned plots (Fig. 1B; 6 May:  $P = 0.0966$ ), equivalent for the second (20 May) sample interval, and greater in non-burned plots by the final two sample dates (3 June:  $P = 0.0777$ ; 17 June:  $P = 0.0011$ ).

Red maple foliar carbohydrates were strongly affected by burning across sample dates (Table 2;  $F = 26.65$ ,  $P = 0.0141$ ), with foliage from trees on burned plots containing significantly lower carbohydrate levels than foliage from trees on non-burned plots. Sample date also affected red maple foliar carbohydrate levels (Fig. 1C;  $F = 13.17$ ,  $P = 0.0001$ ), although there was no difference in foliar carbohydrates in burned versus non-burned red maple foliage for each individual date. Initial carbohydrate concentrations were high and declined dramatically in both burned and non-burned trees by 20 May, increasing slightly during the final two sample intervals.

**Foliar tannins.** There were strongly significant differences among the three species in foliar tannin levels (Table 1;  $F = 547.01$ ,  $P < 0.0001$ ), with the highest levels found in scarlet oak, followed by chestnut oak

and then red maple. Overall foliar tannin levels were marginally lower in foliage from burned trees than foliage from non-burned trees across all three species ( $F = 4.03$ ,  $P = 0.0610$ ), and there were no significant differences between burn treatments for species analyzed individually (Table 2). Foliar tannin concentrations across all species also were affected by sample date ( $F = 24.11$ ,  $P = 0.0001$ ).

Foliar tannins from chestnut oak were strongly affected by sample date ( $F = 54.43$ ,  $P = 0.0001$ ). Tannin levels were relatively high early in the season (Fig. 1D), declining rapidly in the second and subsequent sampling intervals. Tannin concentrations in overstory scarlet oak foliage were also strongly affected by sample date ( $F = 11.42$ ,  $P = 0.0001$ ). Tannins in scarlet oak foliage were highest during the first two sampling intervals and declined steadily as the season progressed (Fig. 1E), but were equivalent on burned and non-burned plots. Similar to the oak species, foliar tannin levels in red maple were affected by sample interval (Fig. 1F;  $F = 7.40$ ,  $P = 0.0014$ ). Tannin levels in red maple foliage increased slightly as the season progressed, whereas foliar tannin levels declined seasonally in the oaks. Foliage from trees on burned plots contained tannin concentrations similar to those on non-burned plots at each sampling date.

**Foliar nutrients.** There were strongly significant species differences in foliar nutrients, with chestnut oak containing higher levels of foliar calcium, magnesium, nitrogen, phosphorous, and fiber than either scarlet oak or red maple (Table 1). The leaf area ratio

Table 2

Characteristics (mean (S.E.)) of canopy chestnut oak, scarlet oak, and red maple on burned and non-burned plots across four sample dates in the Daniel Boone National Forest, Kentucky, 1998<sup>a</sup>

Foliar component	Species	Treatment		<i>F</i>	Pr > <i>F</i>
		Burned	Non-burned		
Carbohydrates (non-structural) (% dry wt)	Chestnut oak	2.48 (0.036) a	2.50 (0.036) a	0.15	0.724
	Scarlet oak	1.98 (0.071) b	2.21 (0.071) a	5.36	0.104
	Red maple	0.90 (0.011) b	0.98 (0.011) a	26.65	0.014
Tannins (% dry wt)	Chestnut oak	0.13 (0.006) a	0.14 (0.006) a	4.00	0.139
	Scarlet oak	0.34 (0.009) a	0.35 (0.009) a	0.78	0.443
	Red maple	0.11 (0.008) a	0.11 (0.008) a	0.58	0.503
Calcium (mg/g dry wt)	Chestnut oak	4.80 (0.283) a	4.83 (0.257) a	0.08	0.937
	Scarlet oak	3.61 (0.136) a	3.33 (0.143) a	0.76	0.457
	Red maple	3.78 (0.217) b	4.60 (0.206) a	2.20	0.041
Magnesium (mg/g dry wt)	Chestnut oak	1.78 (0.054) a	1.83 (0.061) a	0.48	0.634
	Scarlet oak	1.29 (0.032) a	1.31 (0.035) a	0.23	0.818
	Red maple	1.32 (0.046) a	1.37 (0.037) a	0.50	0.624
Nitrogen (mg/g dry wt)	Chestnut oak	25.07 (1.378) a	23.89 (1.444) a	0.83	0.419
	Scarlet oak	18.46 (1.105) a	20.46 (1.282) a	1.39	0.180
	Red maple	15.98 (0.991) a	17.84 (1.104) a	1.29	0.212
Phosphorous (mg/g dry wt)	Chestnut oak	2.40 (0.199) a	2.34 (0.201) a	0.51	0.616
	Scarlet oak	1.62 (0.088) a	1.77 (0.123) a	1.30	0.211
	Red maple	1.62 (0.091) a	1.70 (0.122) a	0.66	0.517
Fiber (acid-digested, % dry wt)	Chestnut oak	35.38 (1.630) a	35.97 (1.326) a	0.28	0.787
	Scarlet oak	35.46 (1.073) a	25.12 (0.789) a	0.25	0.811
	Red maple	26.55 (1.503) a	27.78 (2.029) a	0.49	0.643
Leaf area ratio (cm <sup>2</sup> /g dry wt)	Chestnut oak	214.86 (10.371) a	192.20 (7.445) a	0.13	0.898
	Scarlet oak	166.98 (6.839) a	168.86 (7.877) a	0.07	0.942
	Red maple	216.55 (9.448) a	212.74 (10.408) a	0.33	0.745
Relative basal area growth rate (cm <sup>2</sup> /cm <sup>2</sup> yr)	Chestnut oak	0.021 (0.003) a	0.017 (0.003) a	3.28	0.092
	Scarlet oak	0.014 (0.003) a	0.025 (0.003) b	6.78	0.021
	Red maple	0.032 (0.003) a	0.028 (0.003) b	0.72	0.484

<sup>a</sup> Means within rows followed by the same letter are not significantly different.

(cm<sup>2</sup> g<sup>-1</sup> dry wt) of chestnut oak foliage was equivalent to that of red maple foliage, but exceeded that of scarlet oak ( $F = 15.200$ ,  $P < 0.0001$ ).

Foliar nutrient concentrations in each of the three species were largely unaffected by burning (Table 2). With the exception of calcium in red maple foliage, where non-burned foliage contained greater levels than burned foliage ( $F = 2.20$ ,  $P = 0.041$ ), magnesium, nitrogen and phosphorous levels in foliage from burned trees were equivalent to those of non-burned trees. Sample date was a significant factor affecting nearly all foliar nutrient levels in all three species

(Fig. 1G–R), but these were unaffected by burning. Fiber levels and leaf area ratio were unaffected by burning in all three species (Table 2).

### 3.2. Tree growth

There were significant differences in relative basal area growth rate between the three tree species ( $F = 10.427$ ,  $P = 0.0002$ ), and a significant species  $\times$  burn interaction ( $F = 4.647$ ,  $P = 0.015$ ). The relative basal area growth rate of scarlet oak and chestnut oak were significantly lower than that of red maple

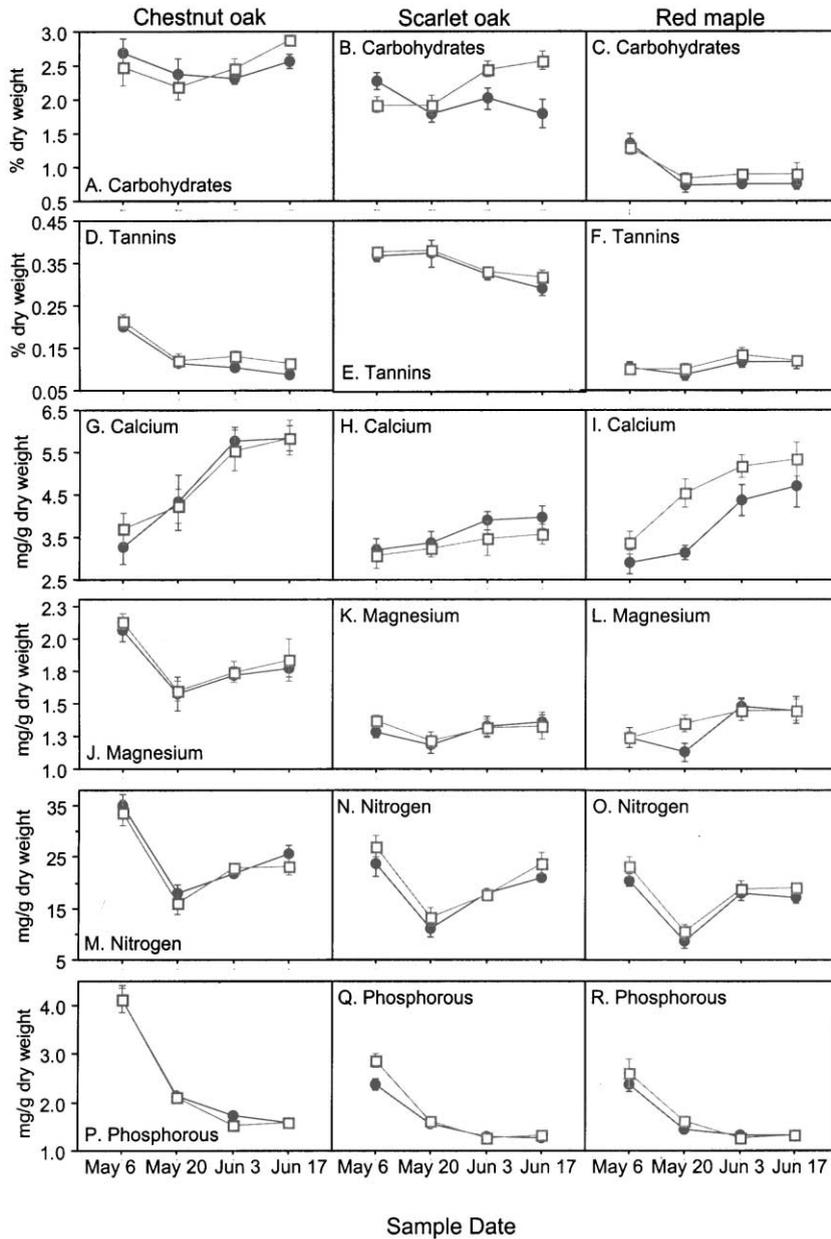


Fig. 1. Seasonal phytochemical characteristics of burned (●) and non-burned (□) canopy chestnut oak, scarlet oak, and red maple in the Daniel Boone National Forest, Kentucky, 1998. Total non-structural carbohydrates (A–C), tannins (D–F), calcium (G–I), magnesium (J–L), nitrogen (M–O), and phosphorous (P–R).

(Table 1). Chestnut oak growth rate was marginally greater on burned plots than on non-burned plots (Table 2;  $F = 3.280, P = 0.0916$ ). In contrast, scarlet oak relative growth rate was significantly lower on

burned plots when compared to non-burned plots ( $F = 6.778, P = 0.0208$ ). There was no significant difference in growth rate between burned and non-burned red maple.

Table 3

Performance of third instar gypsy moth caterpillars fed on foliage collected on 28 May 1998 from canopy scarlet oak and red maple across site treatments (burned and non-burned) in the Daniel Boone National Forest, Kentucky<sup>a</sup>

Insect performance parameter	Scarlet oak	Red maple
Relative growth rate (mg/mg/day)	0.289 (0.021) a	0.124 (0.016) b
Stadium length (day)	6.92 (0.174) b	10.11 (0.415) a

<sup>a</sup> Means within rows followed by the same letter are not significantly different.

Table 4

Performance of third instar gypsy moth caterpillars on canopy scarlet oak and red maple foliage from burned and non-burned sites in the Daniel Boone National Forest, Kentucky<sup>a</sup>

Caterpillar performance	Scarlet oak		Red maple	
	Burned	Non-burned	Burned	Non-burned
Relative growth rate (mg/mg day)	0.301 (0.032) a	0.278 (0.027) a	0.138 (0.022) a	0.107 (0.025) a
Stadium length (day)	6.895 (0.314) a	6.947 (0.143) a	9.850 (0.504) a	10.350 (0.678) a

<sup>a</sup> Means within rows within species followed by the same letter are not significantly different.

### 3.3. Insect assays

Caterpillar performance was assessed on scarlet oak and red maple foliage. Insects fed scarlet oak foliage had relative growth rates over two times greater than did those fed red maple foliage (Table 3;  $F = 38.974, P < 0.0001$ ). Caterpillars fed scarlet oak foliage also developed more rapidly and had a shorter stadium length than did those fed red maple foliage (Table 3;  $F = 49.988, P < 0.0001$ ). There were no significant differences in caterpillar development within either tree species based on burn treatment (Table 4).

## 4. Discussion

The differences in canopy foliar chemistry among the three species were expected. The two oak species contained fairly high levels of foliar total non-structural carbohydrates compared to red maple. Scarlet oak contained over two times the tannin concentration of chestnut oak; red maple had the lowest tannin concentration. Red maple foliage is rich in defensive alkaloids (Barbosa et al., 1990), and tannins, which are not a major component of red maple foliage, most likely play a minor role in red

maple defense. Levels of foliar nutrients (calcium, magnesium, nitrogen and phosphorous) were highest in chestnut oak and intermediate to low in the red maple. Fiber content and leaf area ratio also were greatest in chestnut oak.

The phytochemistry of canopy foliage was largely unaffected by burning. With the exception of decreased non-structural carbohydrates in scarlet oak and red maple foliage, and calcium in red maple foliage, our prescribed fire did not impact levels of the foliar components we measured. Tannin levels were not impacted by burning in any species. Surprisingly we saw no differences in foliar nutrient levels due to burning. Reich et al. (1990) found significant increases in foliar nutrients, including nitrogen, phosphorous, and potassium, following a prescribed fire. However, that studies was conducted with seedling material, whereas our analysis was conducted on foliage sampled from the canopy of older trees.

Tree growth, as measured by relative growth rate of basal area, was greatest in red maple, and equivalent between the two oak species. Red maple growth exceeded that of both oak species on burned and unburned sites, with no growth response to burning. However, burning can easily damage even large red maple trees because of its thin bark (Burns and Honkala, 1990). A more severe burn would very likely

have damaged red maple trees, resulting in reduced growth rates. Chestnut oak relative growth rate responded somewhat positively to burning, whereas scarlet oak growth response to burning was strongly negative. This contrasts with the increased growth rates of both white and chestnut oak found by Boerner et al. (1988) after prescribed burning in the New Jersey Pine Barrens. Lower growth rate of scarlet oak after burning may reflect the concurrent effects of recent droughts; the 1999 growing season had subnormal precipitation, with a Palmer drought index of  $-1.76$  for April 1998–March 1999 (University of Kentucky Agricultural Weather Center, 1999), and scarlet oak on these and other nearby sites, burned and unburned, show greater occurrence of crown die-back than chestnut oak (Arthur, unpublished data).

The differences in gypsy moth caterpillar growth and development between the scarlet oak foliage and red maple foliage were expected. Scarlet oak, a preferred host plant, grew larger insects which developed more quickly than did red maple, a non-preferred host (Leibold et al., 1995). Accelerated larval development allows for avoidance of natural enemies and other mortality factors, and is generally considered a competitive advantage in insects (Price, 1997). Additionally, larger caterpillars tend to develop into larger pupae. In the gypsy moth, pupal weights are directly correlated with fecundity (Drooz, 1985), so that larger insects produce more offspring and are therefore more successful than their smaller counterparts.

Consistent with the phytochemical characteristics, burning did not significantly affect caterpillar performance. Although gypsy moth relative growth rates were greater, and development time less, on burned foliage versus non-burned foliage, these differences were not significant. It is interesting to note, however, that foliar carbohydrates in burned scarlet oak and red maple tended to be less than non-burned foliage, in contrast to studies in other herbivore/plant systems which suggest the phagostimulatory nature of foliar carbohydrates (Thorsteinson, 1960; Schoonhoven, 1968).

The lack of treatment (burn) effects in this study could be due to a number of factors. It is possible that the fire itself was too light to fully combust the litter layer, so that the nutrient release was not large enough to manifest itself in canopy foliar chemistry. Scorch heights were considerably less than 1 m, and scarring

was absent. An additional explanation for the lack of a burn effect may be that mid- to overstory trees are units too large to be affected by late-winter prescribed burning, and the buffering capacity of the tree may exceed our ability to detect any differences.

These results have useful implications with respect to the use of prescribed fire in managing deciduous forest systems to maximize the oak component. Our data are compatible with other studies demonstrating the compromise in red maple performance due to single and repeated fires (Lorimer, 1985; Arthur et al., 1998). Our data also suggest that foliar palatability to some herbivorous insects, including outbreak species such as the gypsy moth, may be unaffected by burning, and that managers making decisions regarding prescriptions need not worry about enhancing forest stand susceptibility to outbreak defoliators with light, late-winter burning.

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### References

- Abrams, M., 1992. Fire and the development of oak forests. *BioScience* 42, 346–353.
- Adams, A.S., Rieske, L.K., 2001. The effects of fire on oak seedling growth and herbivore interactions. *For. Sci.*
- Arthur, M.A., Paratley, R.D., Blankenship, B.A., 1998. Single and repeated fires affect survival and regeneration of woody and herbaceous species in an oak–pine forest. *J. Torr. Bot. Soc.* 125, 225–236.
- Baldwin, I.T., Schultz, J.C., 1983. Rapid changes in tree leaf chemistry induced by damage: evidence for communication between plants. *Science* 221, 277–279.

- Barbosa, P., Gross, P., Provan, G.J., Pacheco, D.Y., Stermitz, F.R., 1990. Allelochemicals in foliage of unfavored tree hosts of the gypsy moth, *Lymantria dispar* L. 1. Alkaloids and other components of *Liriodendron tulipifera* L. (Magnoliaceae), *Acer rubrum* L. (Aceraceae) and *Cornus florida* L. (Cornaceae). J. Chem. Ecol. 16, 1719–1730.
- Beck, D.E., Hooper, R.M., 1986. Development of a southern Appalachian hardwood stand after clearcutting. South. J. Appl. For. 10, 168–172.
- Blankenship, B., Arthur, M.A., 1999. Soil nutrient and microbial response to prescribed fire in an oak–pine ecosystem in eastern Kentucky. In: Stringer, J.W., Loftis, D.L. (Eds.), Proceedings of the 12th Central Hardwood Forest Conference, February 28–March 2, 1999, Lexington, KY. US For. Serv. Gen. Tech. Rep. SRS-24, Asheville, NC.
- Boerner, R.E.J., Lord, T.R., Peterson, J.C., 1988. Prescribed burning in the oak–pine forest of the New Jersey Pine Barrens: effects on growth and nutrient dynamics of two *Quercus* species. Am. Midl. Nat. 120, 108–119.
- Braun, E.L., 1950. Deciduous Forests of Eastern North America. Hafner, New York.
- Burns, R.M., Honkala, B.H., 1990. Silvics of North America. 2: Hardwoods. US Department of Agricultural Handbook No. 654, Vol. 2. USDA, Washington, DC.
- Campbell, R.W., Sloan, R.J., 1977. Forest stand responses to defoliation by the gypsy moth. For. Sci. Monogr. 19, 34.
- Carvell, K.L., Tyron, E.H., 1961. The effect of environmental factors on the abundance of oak regeneration beneath mature stands. For. Sci. 7, 98–105.
- Davidson, C.B., Gottschalk, K.W., Johnson, J.E., 1999. Tree mortality following defoliation by the European gypsy moth (*Lymantria dispar* L.) in the United States: a review. For. Sci. 45, 74–84.
- Delcourt, P.A., Delcourt, H.R., 1998. The influence of prehistoric human-set fires on oak–chestnut forests in the southern Appalachians. Castanea 63, 337–345.
- Drooz, A.T., 1985. Insects of eastern forests. US For. Serv. Misc. Publ. No. 1426. Washington, DC, 608 pp.
- Dudt, J.F., Shure, D.J., 1994. The influence of light and nutrients on foliar phenolics and insect herbivory. Ecology 75, 86–98.
- Fajvan, M.A., Wood, J.M., 1996. Stand structure and development after gypsy moth defoliation in the Appalachian Plateau. For. Ecol. Manage. 89, 79–88.
- Gammon, A.D., Rudolph, V.J., Arend, J.L., 1960. Regeneration following clearcutting of oak during a seed year. J. For. 58, 711–715.
- Gottschalk, K.W., 1985. Effects of shading on growth and development of northern red oak, black oak, black cherry, and red maple seedlings. I. Height, diameter, and root/shoot ratio. In: Dawson, J.O., Majerus, K.A. (Eds.), Proceedings of the Fifth Central Hardwood Forest Conference, Urbana-Champaign, IL, SAF Publ. 85-05, University of Illinois, pp. 189–195.
- Gottschalk, K.W., 1993. Gypsy moth effects on mast production. In: McGee, C.E. (Ed.), Proceedings of the Southern Appalachian Mast Management Workshop. University of Tennessee, Knoxville, August 14–16, 1986.
- Hagerman, A.E., 1987. Radial diffusion method for determining tannin in plant extracts. J. Chem. Ecol. 13, 437–449.
- Haukioja, E., Ruohomaki, K., Senn, J., Suomela, J., Walls, M., 1990. Consequences of herbivory in the mountain birch (*Betula pubescens* ssp. *tortuosa*): importance of the functional organization of the tree. Oecologia 82, 238–247.
- Hunt, R., 1990. Basic Growth Analysis: Plant Growth for Beginners. Unwin Hyman, London.
- Hunter, M.D., Schultz, J.C., 1995. Fertilization mitigates chemical induction and herbivore responses within damaged oak trees. Ecology 76, 1226–1232.
- Isaac, R.A., Johnson, W.C., 1976. Determination of total nitrogen in plant tissue, using a block digester. J. AOAC 59, 98–100.
- Leibhold, A.M., Gottschalk, K.W., Muzika, R.M., Montgomery, M.E., Young, R., O'Day, K., Kelley, B., 1995. Suitability of North American trees species to gypsy moth: a summary of field and laboratory tests. Gen. Tech. Rep. NE-211. US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, PA.
- Lorimer, C.G., 1985. The role of fire in the perpetuation of oak forests. In: Johnson, J.E. (Ed.), Challenges in Oak Management and Utilization. Univ. Wisc. Coop. Ext. Serv., Madison, WI, pp. 8–25.
- Lorimer, C.G., 1989. The oak regeneration problem: new evidence on causes and possible solutions. In: Proceedings of the Annual Symposium of the Hardwood Research Council, Memphis, TN, pp. 23–40.
- Muick, P.C., Bartolome, J.W., 1987. Factors associated with oak regeneration in California. Gen. Tech. Rep. PSW-100. Pacific Southwest Forest and Range Experiment Station, US Department of Agriculture, Forest Service, Berkeley, CA.
- Price, P.W., 1991. The plant vigor hypothesis and herbivore attack. Oikos 62, 24–251.
- Price, P.W., 1997. Insect Ecology, 3rd Edition. Wiley, New York, Oikos 62, 244–251.
- Prieto-Fernandez, A., Villar, M.C., Carballas, M., Carballas, T., 1993. Short-term effects of a wildfire on the nitrogen status and its mineralization kinetics in an Atlantic forest soil. Soil Biol. Biochem. 25, 1657–1664.
- Quarmby, C., Allen, S.E., 1989. Organic constituents. In: Allen, S.E. (Ed.), Chemical Analysis of Ecological Materials. Wiley, New York, pp. 160–201.
- Reich, P.B., Abrams, M.D., Ellsworth, D.S., Kruger, E.L., Tabone, T.J., 1990. Fire affects ecophysiology and community dynamics of central Wisconsin oak forest regeneration. Ecology 71, 2179–2190.
- Rieske, L.K., Raffa, K.F., 1998. Interactions among insect herbivore guilds: influence of thrips bud injury on foliar chemistry and suitability to gypsy moths. J. Chem. Ecol. 24, 501–523.
- Roth, S.K., Lindroth, R.L., Montgomery, M.E., 1994. Effect of foliar phenolics and ascorbic acid on performance of the gypsy moth (*Lymantria dispar*). Biochem. Syst. Ecol. 22, 341–351.
- SAS Institute, 1997. SAS/STAT Software: Changes and Enhancements through Release 6.12. SAS Institute, Cary, NC.
- Schoonhoven, L.M., 1968. Chemosensory bases of host plant selection. Annu. Rev. Entomol. 13, 115–136.

- Schultz, J.C., 1988. Many factors influence the evolution of herbivore diets, but plant chemistry is central. *Ecology* 69, 896–897.
- Siemann, E., Haarstad, J., Tilman, D., 1997. Short-term and long-term effects of burning of oak savanna arthropods. *Am. Midl. Nat.* 137, 349–361.
- Thorsteinson, A.J., 1960. Host selection in phytophagous insects. *Annu. Rev. Entomol.* 5, 193–218.
- USDA Forest Service, 1991. Gypsy moth: a balanced perspective. USDA Forest Service Video, Southern Region, Forest Pest Management.
- University of Kentucky Agricultural Weather Center, 1999. Department of Biosystems and Agricultural Engineering, College of Agriculture, Lexington, KY. [www: agvx.ca.uky.edu/all\\_ky\\_rain.txt](http://www.agvx.ca.uky.edu/all_ky_rain.txt).