Uneven-aged and even-aged logging alter foliar phenolics of oak trees remaining in forested habitat matrix

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Abstract

Despite potential links between logging-induced changes in abiotic factors, variation in plant secondary chemistry, and foliage consumption by herbivores, few studies have investigated the impacts of timber extraction on plant anti-herbivore metabolites. To determine if uneven-aged (UAM, i.e., selective logging) and even-aged (EAM, i.e., clear-cutting) management regimes impacted levels of foliar phenolics in *Quercus alba* and *Q. velutina* (white and black oak, respectively), we quantified the levels of condensed tannins (CT) and total phenolics in the leaves of canopy and understory trees located within landscapes undergoing UAM, EAM, or no harvest (NHM) in the southeastern Missouri Ozarks. In the understory, total phenolics were slightly elevated in *Q. velutina* trees in UAM relative to trees in NHM and EAM sites but lower in *Q. alba* trees in EAM relative to trees in UAM and NHM sites. Furthermore, treatment effects on understory total phenolic concentrations were greater in older forests. In the canopy, treatments altered plant chemistry only for trees in block 2, where CT concentrations were elevated in trees within UAM and EAM sites relative to NHM for *Q. alba*, but elevated in UAM and reduced in EAM relative to NHM for *Q. velutina*. Understory trees of both species had higher levels of both CT and total phenolics when growing on slopes with south- and west-facing aspects than on those with north- and east-facing aspects. Our results indicate that timber harvests, even at low levels of extraction (10% biomass removal), altered concentrations of foliar polyphenolics in *Q. alba* and *Q. velutina* but that the effects of logging on phenolics were dependent on blocking factors (forest age and previous management history). In addition, defoliation levels generally were lower where concentrations of phenolics where higher (e.g. in the canopy and on south- and west-facing slopes). In combination with additional studies of the impacts of phenolics on oak herbivores, as well as studies of the impacts of herbivores on oak growth, our results indicate that changes in foliar chemistry due to forest management practices may have large consequences for Ozark forest communities.
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Keywords: Canopy; Clear-cutting; Foliar chemistry; Phenolics; *Quercus*; Selective logging

1. Introduction

Human disturbances, including timber management practices, can profoundly impact soil nutrient quantities (Dupouey et al., 2002), light levels, and plant growth rates (Greiser Johns, 1997; Barbosa and Wagner, 1989). Each of these factors may influence plant anti-herbivore defense levels, either through tradeoffs among nutrient availability, plant growth, and allocation to carbon-based defenses (Bryant et al., 1983; Coley et al., 1985) or via tradeoffs between growth and defense in general (Herms and Mattson, 1992; Jones and Hartley, 1999). Defensive plant metabolites structure insect herbivore communities

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(Abrahamson et al., 2003), influence defoliation levels (Wold and Marquis, 1997), and affect interactions between pest species and their natural enemies (Rossiter et al., 1988). Thus, changes in levels of anti-herbivore compounds as a result of disturbance may alter plant–herbivore interactions, subsequent plant abundance, and factors critical to the sustainability of timber harvests, such as timber biomass accumulation and nutrient cycling. For example, changes in defensive metabolites can directly or indirectly (via natural enemies) alter the distribution and abundance of herbivores, resulting in changes in plant consumption, timing and quantity of litter fall, and inputs of insect excrement to the forest floor (Hunter et al., 2003). Furthermore, changes in defensive compounds, specifically polyphenolics, can directly alter plant litter quality, which influences decomposition, humification, and nutrient mineralization and uptake rates (Horner et al., 1988; Hättenschwiler and Vitousek, 2000; Madritch and Hunter, 2002). These changes may feed back to alter future plant growth or defense investment (Belovsky and Slade, 2000).

Despite these links between disturbance, plant defense, herbivory, and ecosystem function, few studies have investigated the impacts of timber harvesting on anti-herbivore metabolites (but see Shure and Wilson, 1993; Ganzhorn, 1995; Covelo and Gallardo, 2001). Moreover, evaluation of alternative timber extraction regimes for the purpose of choosing sustainable forest management practices (Brookshire and Hauser, 1993) has largely overlooked impacts on plant anti-herbivore chemistry. Natural resource managers propose that practices such as reduced impact logging or selective harvesting (uneven-aged management) are more sustainable alternatives to clear-cutting (even-aged management) because they retain a partial canopy, reduce soil erosion or compaction, and more closely approximate mature forest structure (Haight, 1987; Greiser Johns, 1997; Fig. 1).

In the Ozarks of southeastern Missouri, long-term research is currently underway to evaluate the sustainability of uneven-aged (UAM) and even-aged (EAM) management practices (Gram et al., 2001; Shifley and Kabrick, 2002). Seventy-two percent of the biomass of
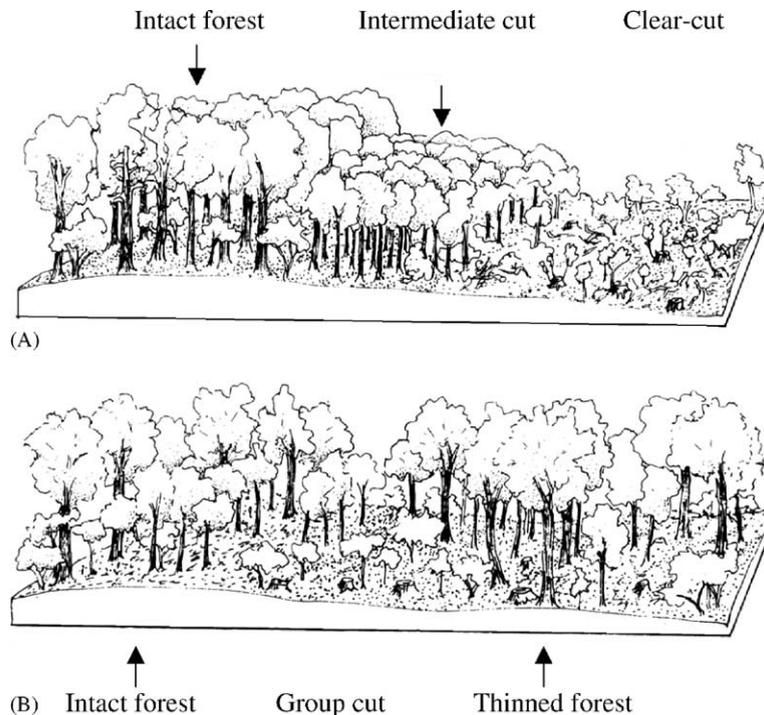

Fig. 1. Forest structure under (A) even-aged and (B) uneven-aged forest management timber harvest regimes. Arrows indicate location of stands of trees sampled in this study. Diagram modified from Missouri Department of Conservation (1994).

Ozark forests in this region is oak (Grabner et al., 1997; J. Kabrick, personal communication), and species of *Quercus* are both important timber resources and dominant tree species in many other North American forests. Previous studies in this system demonstrated that oaks are hosts to more than 260 species of leaf-chewing herbivores (Forkner et al., unpublished data) and that leaf consumption by these herbivores can reduce yearly biomass accumulation by as much as 30% (Marquis and Whelan, 1994). Polyphenolics, which include hydrolysable and condensed tannins, are generally thought to be the predominant anti-herbivore defenses in oaks, and studies demonstrate negative correlations between polyphenolics and the abundance and performance of herbivorous insects (Feeny, 1970; Schultz, 1989; Forkner et al., 2004). Because EAM and UAM differ considerably in their impacts on soil nutrients, temperature and light regimes, plant spacing, edge habitat, and canopy retention for both the harvested areas and the remaining matrix of forest, they may also differ in their impacts on oak polyphenolics. Determining the impact of these management practices on plant chemistry is an important part of evaluating the long-term sustainability of timber harvest methods in oak-dominated forests.

Phenolics show both temporal and spatial variability that may influence their patterns of response to logging. *Quercus* condensed tannins generally increase over the course of the growing season (Feeny, 1970; Shure and Wilson, 1993; Forkner et al., 2004). Initially, levels of nitrogen and water are high and phenolics concentrations are low in newly emerging leaves. We predicted, therefore, that the impact of timber removal on phenolics would be more apparent after leaves had hardened and differences in resource availability between trees in different treatments were expressed. In addition to being temporally variable, phenolics are higher in high light environments than in shady understory habitats (Dudt and Shure, 1994). Thus, we predicted that trees in the remaining forest matrix of UAM sites would show higher levels of phenolics than trees in the unlogged areas of EAM sites because UAM creates a more open and uneven canopy structure (Fig. 1), increasing the probability that an understory sapling or branch will intercept sunlight. We also predicted that changes in phenolics in response to logging would be greater in understory

leaves compared to leaves in high light environments of tree canopies, where phenolic production may already be at its physiological maximum. Finally, phenolics vary greatly in identity and concentration among plant species, even among congeners (Ayers et al., 1997). Because the biological activity of a tannin relates to its chemical structure (Bettolo et al., 1986; Clausen et al., 1992; Zucker, 1983; Ayers et al., 1997) and because species vary in their abilities to respond to abiotic variation, we predicted that the impact of logging on phenolics would vary among plant species.

Whereas higher light levels may increase levels of polyphenolics, two other mechanisms, increased plant growth and increased soil nutrient availability, might causes decreases in phenolics levels. UAM generally provides more productive plant spacing (Barbosa and Wagner, 1989), and with additional light resources and less competition from conspecifics, plants in thinned areas of UAM sites might have more rapid growth. If tradeoffs exist between growth rates and allocation to defense (Jones and Hartley, 1999), then oaks in UAM sites may have lower levels of phenolics than oaks in NHM and unharvested sites in EAM landscapes. Likewise, soil nitrogen availability can increase in thinned forests (David, 1997), and increased nutrient availability can decrease phenolic concentrations (Hunter and Schultz, 1995; Forkner and Hunter, 2000). The degree to which increases in phenolics due to increased insolation will overwhelm potential decreases due to increased growth rates and greater nutrient availability is unclear. Results from Dudt and Shure (1994) and Hunter and Forkner (1999), however, suggest that the importance of light to phenolic concentrations may overwhelm the influence of soil nutrients, as the effects of the latter tend to be more ephemeral and spatially variable. If, on the other hand, these factors have a greater effect than do changes in light levels, we would predict that foliar phenolics would be lowest in trees in UAM landscapes.

Our objectives in this study were to determine if timber harvesting alters foliar concentrations of total phenolics and condensed tannins (CT) in *Quercus alba* and *Q. velutina* (white oak and black oak, respectively) trees that remain after timber extraction and if the impacts of timber removal on phenolics differed between clear-cutting (EAM) and selective logging (UAM). To that end, we collected leaves for

spectrophotometric assays from canopy and understory trees of *Q. velutina* and *Q. alba* in stands within harvested and unharvested landscapes in southeastern Missouri Ozarks forests. In addition, we measured defoliation levels to determine the degree to which treatments impacted levels of herbivory. We predicted that (1) trees in EAM and UAM landscapes would differ from trees in NHM landscapes in concentration of phenolics, with trees in UAM sites having the greater difference relative to controls; (2) trees in treated (EAM and UAM) and untreated (NHM) landscapes would have similar levels of polyphenolics immediately after budburst, but impacts of timber harvest on polyphenolics would be apparent later in the season; (3) differences between the impacts of UAM and EAM on phenolics would be greater in the understory than in the high light environment of the forest canopy; and (4) both *Q. alba* and *Q. velutina* would show changes in foliar phenolics as a result of timber harvest, but responses would be species-specific.

2. Study area

Initiated in 1989 by the Missouri Department of Conservation, the Missouri Ozark Forest Ecosystem Project (MOFEP) is a landscape-level, long-term, multi-investigator experiment. MOFEP uses a randomized complete block design to evaluate the effects of even-aged management, uneven-aged management, and no harvest management (NHM) on multiple abiotic and biotic ecosystem attributes, including diversity of forest interior birds, small mammals, ground flora, lichens, leaf litter arthropods, and herpetofauna; berry and acorn production; stump sprout response; microclimate characteristics; and aspects of carbon and sulfur transformations (Kurzejeski et al., 1993; Brookshire et al., 1997). MOFEP is envisioned as a 100-year study with timber harvests beginning in 1996 and repeated at 15-year intervals. MOFEP study sites are located in southeast Missouri and encompass nearly 18,000 ha of Shannon, Reynolds, and Carter counties, between 37°00′ and 37°12′N and 91°01′ and 91°13′W. This area is primarily mature upland oak–hickory and oak–pine communities and is 84% forested (Brookshire and Hauser, 1993; Xu et al., 1997). *Q. alba* (white oak) and *Q. velutina* (black

oak), along with *Q. coccinea* (scarlet oak), dominate the canopy. *Q. alba*, *Q. velutina*, *Cornus florida*, and *Sassafras albidum* constitute the majority of woody understory species.

3. Methods

3.1. Logging

The overall experimental design includes nine forested sites (three sites within each of three blocks), ranging in size from 266 to 527 ha. Sites were chosen and blocked based on forest age, vegetation, and soil composition (block 1: sites 1, 2, 3; block 2: sites 4, 5, 6; block 3: sites 7, 8, 9; Fig. 2). Specifics of site selection are outlined in Brookshire et al. (1997) and Sheriff and He (1997). Entire sites within blocks were randomly assigned to one of three cutting regimes: EAM, UAM, or NHM (Fig. 2). Sites were subdivided into stands, averaging 4 ha in size, of similar ecological land types (ELTs) defined by slope, aspect, vegetation composition, and soil type. Removal of 10% of forest biomass occurs at each harvest, resulting in landscapes having both logged areas and remaining, untreated forest. In order to conduct timber sales, stands to be cut within EAM sites were chosen such that the size class distribution of remaining forest contained 10% seedlings, 20% trees 6–14 cm dbh, 30% trees 14–29 cm dbh, and 40% saw timber (trees >29 cm dbh). To accomplish this distribution, some stands were clear-cut and others were treated with intermediate cutting following Roach and Gingrich (1968) (Fig. 1). Stands within UAM sites were chosen such that the largest tree diameter objective for UAM sites was equal to the desired saw timber size objective for EAM sites, and the target size class distribution in UAM sites was identical to the composite size class distribution in EAM sites (Brookshire et al., 1997). Trees to be harvested in UAM sites were removed in small groups (''group cuttings''), individually, or girdled and left standing. Ten percent of each EAM and UAM site was designated as ''old-growth'' and not available for harvest. NHM sites are not subjected to manipulation, except that wildfires and large-scale insect outbreaks, should they occur, would be suppressed. NHM sites serve as experimental controls in this project (Sheriff and He, 1997). Prior to MOFEP,
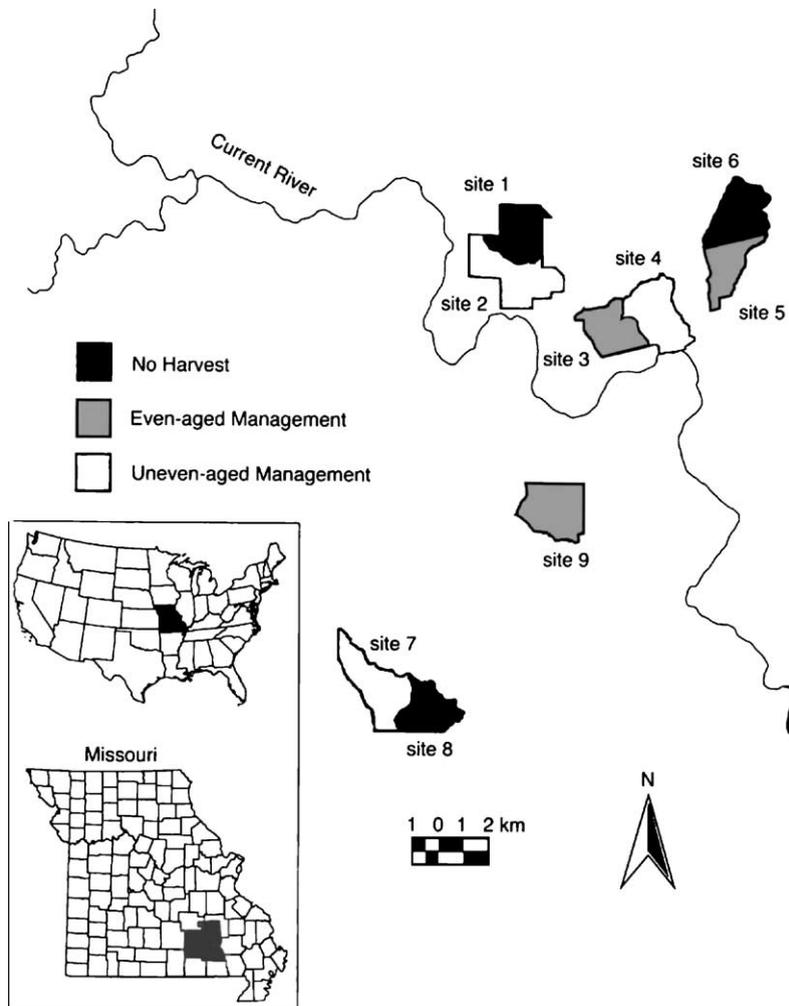
Fig. 2. Location and assignment of timber harvest treatments in the Missouri Ozark Forest Ecosystem Project.

no harvesting had occurred at least since 1950, and most overstory trees were 50–70 years old. Forests in blocks 1–3 were acquired by the Missouri Department of Conservation as early as 1938, 1925, 1952, respectively. At the time of acquisition, anthropogenic disturbances were reduced or eliminated, such that forests of block 2 are the oldest and those in block 3 the youngest.

Data presented here are for ground-level foliage (<2.5 m) from a mixture of sapling and low hanging branches of sub-canopy and canopy trees on ELTs 17 and 18 (south- and west-facing and north- and east-facing aspects, respectively) and canopy foliage (>15–

20 m) from trees along ridge tops (ELT 11). Previous chemical analyses indicated average concentrations of CT in foliage from understory saplings did not differ from that in foliage from low hanging understory branches (Forkner et al., 2004). We were restricted to canopy trees in ELT 11 and in blocks 1 and 2 because we used a bucket truck to gain access to the canopy, and roads wide enough for bucket truck access were primarily along ridge tops in these blocks. We only sampled canopy trees in areas where a closed canopy existed over the road. ELTs 11, 17, and 18 constitute 90% of the total MOFEP area (Xu et al., 1997).

3.2. Chemical assays

Foliage for chemical analyses was collected in 2001, 5 years after the first timber harvests. This allowed us to assess treatment differences that were the result of longer-term, logging-induced changes in forest overstory structure, plant spacing, and nutrient cycling, rather than assessing differences that were the short-term result of wound-induced responses to branch damage during timber extraction.

We collected leaf material in early May, late June, and late August of 2001. We collected three to five leaves from canopy branches of three trees each of *Q. alba* and *Q. velutina* within two stands in each of six sites ($n = 12$ trees/oak species per treatment). In the understory we collected three to five leaves from three saplings or low hanging branches of each oak species within four stands each in all nine sites ($n = 108$ trees/oak species per treatment). *Quercus velutina* did not occur in the understory of all stands, so sample sizes are less than for *Q. alba* ($n = 102-108$ trees per treatment). Leaves were flash-frozen in liquid nitrogen as they were collected, returned to the laboratory on dry ice, lyophilized, ground to a fine powder, and stored at $-80\,°C$.

Condensed tannins were assayed using a microscale modification of the acid–butanol technique (Rossiter et al., 1988). Total phenolics were estimated using a microscale modification of the Folin–Denis technique (Folin and Denis, 1912; Waterman and Mole, 1994). The Folin–Denis assay measures the total concentration of phenolic hydroxyl groups, and, therefore, includes both condensed and hydrolysable tannins. Standards were generated separately for each oak species by purifying aqueous extracts of pooled leaf tissue from all census dates with multiple washes of 95% ethanol followed by 70% aqueous acetone on Sephadex LH-20 in a Büchner funnel. Acetone was removed by rotary evaporation, and aqueous extracts were lyophilized to yield dry, purified oak tannin. Concentrations of phenolics are expressed as percent dry mass oak condensed tannin or total oak phenolic equivalents.

3.3. Defoliation estimates

At the end of the growing season in 2000, we assessed trees for accumulated levels of insect defoliation. Following procedures similar to Hunter (1987) and Hunter and Schultz (1993, 1995), we inspected a haphazardly chosen sample of at least 30 leaves per tree and classified them into one of seven damage classes representing percent leaf area removed (LAR): undamaged, 0–10, 10–25, 25–50, 50–75, 75–90, and >90%. We then averaged these LAR values to generate a single estimate of leaf damage for each tree. As with leaf collections for chemical assays, we examined three trees of each oak species within four understory stands each in all nine sites ($n = 108$ trees/oak species per treatment). In the canopy, we examined three trees of each species in two stands in each of three sites (only block 2, $n = 18$ trees/oak species).

3.4. Statistical analyses

Treatment effects were analyzed using repeated measures analysis of variance (ANOVA) in SAS (1999). ANOVAs were performed separately for each stratum. Phenolic concentrations and percent LAR values were arcsine square root transformed to meet assumptions of normality. Multivariate results, rather than Greenhouse-Geisser adjusted univariate results, of repeated measures ANOVA are presented. Oak species, logging treatment and block were main effects. Slope aspect was a split-plot factor, and stands were nested within treatment, block, and slope. We considered logging treatments and oak species to be fixed effects and block to be a random effect. Blocks essentially represented forests of different ages and soil types, giving us an a priori reason to believe that a treatment by block interaction was likely. Thus, the main effects of oak and treatment were tested over their interaction with block (Newman et al., 1997). We followed procedures outlined in Zar (1984) to determine the appropriate $MS_{denominator}$ terms for calculations of F statistics. Because textbooks differ in their prescriptions for error terms for calculation of F ratios (Newman et al., 1997), however, we also give results of tests for treatment effects in which we use the whole-plot error rather than interactions with block for calculation of F ratios.

4. Results

4.1. Oak species

The average concentration of CT in the foliage of understory *Q. alba* was $3.4 \pm 0.1\%$ dry mass in May,

and it increased significantly by 3–4% at each census (month effect, Table 1, Fig. 3). Concentrations of CT in understory *Q. alba* were more than twice that in the leaves of understory *Q. velutina* in May (1.6 ± 0.1% dry mass for *Q. velutina*), and remained higher at all leaf collection dates (significant oak effect, Table 1). Whereas levels of CT in *Q. alba* continued to increase, concentrations in understory *Q. velutina* remained at nearly 5% dry mass from mid-June until the end of the season (marginally significant month × oak interaction, Table 1, Fig. 3). Concentrations of understory total phenolics in the foliage of *Q. alba*, which measured approximately 16.0 ± 1.0% dry mass in all

months, were also higher than levels in the foliage of *Q. velutina* (significant oak effect, Table 1), which ranged from 14.5 ± 0.6% in May to 11.6 ± 0.3% dry mass in late August in *Q. velutina*.

May canopy CT concentrations increased significantly from 7.5 ± 0.4 and 3.8 ± 0.2% dry mass for *Q. velutina* and *Q. alba*, respectively, to 14.2 ± 1.5% in mid-June and late August in both species (significant month effect, Table 2). Although there was no main effect of oak species on concentrations of either CT or total phenolics, total phenolics levels declined from 15.6 ± 0.7% in May to 14.0 ± 0.7% in August for *Q. velutina* but increased from 18.2 ± 0.7 to 22.2 ± 0.7%
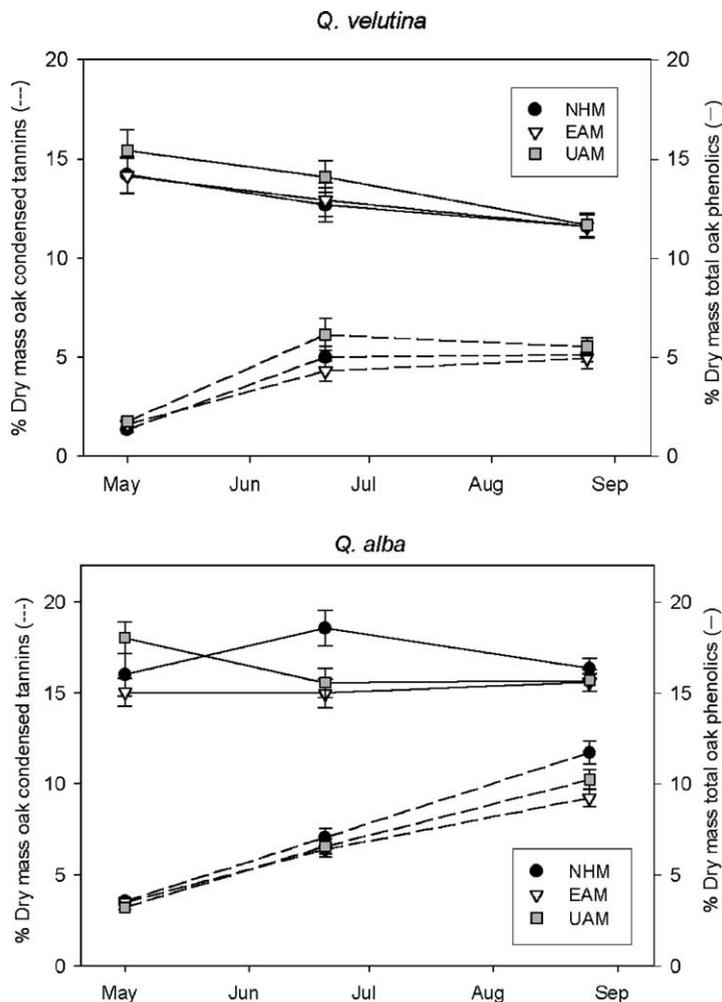

Fig. 3. Mean (±S.E.) percent dry mass oak condensed tannins and total phenolics in understory *Q. velutina* and *Q. alba* in NHM, EAM, and UAM treatments.

Table 1
Results from repeated measures ANOVA for understory concentrations of condensed tannins and total phenolics

Source	MS_{den}	d.f.	Condensed tannins		Total phenolics	
			F	P	F	P
Between subject effects						
Oak species (O)	$MS_{O \times B}$	1	89.01	0.0110	30.94	0.0308
Treatment (T)	$MS_{T \times B}$	2	3.14	0.1512	2.30	0.2161
Block (B)	$MS_{O \times T \times B}$	2	12.51	0.0190	21.91	0.0070
O × T	$MS_{O \times T \times B}$	2	2.47	0.2005	24.56	0.0056
O × B	$MS_{O \times T \times B}$	2	2.26	0.2204	25.91	0.0051
T × B	$MS_{O \times T \times B}$	4	0.85	0.5595	14.75	0.0116
O × T × B (whole-plot error)		4				
Slope (S)	$MS_{Stand(T \times B \times S)}$	1	5.04	0.0376	4.99	0.0384
T × S	$MS_{Stand(T \times B \times S)}$	2	0.26	0.7766	1.31	0.2939
B × S	$MS_{O \times Stand(T \times B \times S)}$	2	0.81	0.4621	0.90	0.4248
O × S	$MS_{O \times Stand(T \times B \times S)}$	1	0.16	0.6901	0.68	0.4217
O × T × S	$MS_{O \times Stand(T \times B \times S)}$	2	0.43	0.6567	1.10	0.3581
O × B × S	$MS_{O \times Stand(T \times B \times S)}$	2	0.47	0.6312	1.00	0.3900
T × B × S	MS_{error}	4	1.18	0.3229	0.27	0.8954
O × T × B × S	MS_{error}	3	3.79	0.0119	2.09	0.1047
Stand (T × B × S)	MS_{error}	18	2.48	0.0016	2.62	0.0008
O × Stand (T × B × S)	MS_{error}	16	1.95	0.0204	1.33	0.1895
Error (split-plot error)		138				

Source	MS_{den}	$N_{d.f.}/D_{d.f.}$[a]	Condensed tannins		Total phenolics	
			F	P	F	P
Within subject effects[b]						
Month (M)	MS_{error}	2/137	454.74	<0.0001	9.22	0.0002
M × O	$MS_{M \times O \times B}$	2/1	141.21	0.0594	2.08	0.4405
M × T	$MS_{M \times T \times B}$	4/6	2.46	0.1560	0.60	0.6755
M × O × T	$MS_{M \times O \times T \times B}$	4/6	1.98	0.2170	0.64	0.6533
M × B	$MS_{M \times O \times T \times B}$	4/6	6.64	0.0215	6.77	0.0206
M × O × B	$MS_{M \times O \times T \times B}$	4/6	0.39	0.8125	0.84	0.5495
M × T × B	$MS_{M \times O \times T \times B}$	8/6	1.36	0.3632	2.19	0.1775
M × O × T × B	MS_{error}	8/274	0.49	0.8602	0.99	0.4461
M × S	$MS_{M \times Stand(T \times B \times S)}$	2/17	3.56	0.0512	0.47	0.6311
M × O × S	$MS_{M \times O \times Stand(T \times B \times S)}$	2/15	0.08	0.9278	0.44	0.6526
M × T × S	$MS_{M \times Stand(T \times B \times S)}$	4/34	0.32	0.8654	0.45	0.7702
M × O × T × S	$MS_{M \times O \times Stand(T \times B \times S)}$	4/30	0.80	0.5365	1.40	0.2566
M × B × S	$MS_{M \times O \times Stand(T \times B \times S)}$	4/30	1.45	0.2412	1.53	0.2181
M × O × B × S	$MS_{M \times O \times Stand(T \times B \times S)}$	4/30	0.42	0.7922	3.73	0.0141
M × T × B × S	MS_{error}	8/274	0.81	0.5946	0.64	0.7400
M × O × T × B × S	MS_{error}	6/274	1.13	0.3431	0.76	0.5991
M × Stand (T × B × S)	MS_{error}	36/274	1.31	0.1192	1.33	0.1102
M × O × Stand (T × B × S)	MS_{error}	32/274	0.83	0.7354	0.49	0.9914
Error		276				

[a] Numerator degrees of freedom/denominator degrees of freedom.
[b] Results for within subject effects are Wilks' lambda test statistics from MANOVA.

Table 2
Results from repeated measures ANOVA for canopy concentrations of condensed tannins and total phenolics

Source	MS$_{den}$	d.f.	Condensed tannins		Total phenolics	
			F	P	F	P
Between subject effects						
Oak species (O)	MS$_{O \times B}$	1	39.35	0.1006	25.29	0.1250
Treatment (T)	MS$_{T \times B}$	2	1.37	0.4218	0.76	0.5684
Block (B)	MS$_{Stand(T \times B)}$	1	2.06	0.2012	0.00	0.9892
O × T	MS$_{O \times T \times B}$	2	1.83	0.3532	1.46	0.4071
O × B	MS$_{O \times Stand(T \times B)}$	1	0.38	0.5609	9.95	0.0197
T × B	MS$_{Stand(T \times B)}$	2	7.27	0.0249	1.69	0.2613
O × T × B	MS$_{O \times Stand(T \times B)}$	2	2.46	0.1658	1.18	0.3692
Stand (T × B)	MS$_{error}$	6	0.53	0.7830	2.18	0.0614
O × Stand (T × B)	MS$_{error}$	6	0.25	0.9553	0.67	0.6709
Error		47				

Source	MS$_{den}$	N$_{d.f.}$/D$_{d.f.}$[a]	Condensed tannins		Total phenolics	
			F	P	F	P
Within subject effects[b]						
Month (M)	MS$_{error}$	2/46	94.84	<0.0001	1.62	0.2008
M × O	MS$_{M \times O \times B}$	2/2[c]	16.57	0.0569	83.39	0.0118
M × T	MS$_{M \times T \times B}$	4/2	4.41	0.1933	0.48	0.7620
M × O × T	MS$_{M \times O \times T \times B}$	4/2	1.43	0.4516	4.26	0.1991
M × B	MS$_{M \times Stand(T \times B)}$	2/5	1.11	0.3996	1.19	0.3768
M × O × B	MS$_{M \times O \times Stand(T \times B)}$	2/5	1.62	0.2863	0.56	0.6021
M × T × B	MS$_{M \times Stand(T \times B)}$	4/10	1.06	0.4264	1.72	0.2216
M × O × T × B	MS$_{M \times O \times Stand(T \times B)}$	4/10	3.82	0.0390	0.21	0.9272
M × Stand (T × B)	MS$_{error}$	12/92	1.69	0.0823	2.27	0.0142
M × O × Stand (T × B)	MS$_{error}$	12/92	0.41	0.9563	0.81	0.6365
Error		94				

[a] Numerator degrees of freedom/denominator degrees of freedom.
[b] Results for within subject effects are Wilks' lambda test statistics from MANOVA.
[c] Insufficient degrees of freedom for multivariate test, univariate results reported.

over the same time period in *Q. alba* (significant month × oak effect, Table 2).

4.2. Treatment effects

Concentrations of understory total phenolics in *Q. velutina* were slightly (1% dry mass) elevated in trees in UAM compared to those in EAM and NHM sites. In contrast, concentrations in *Q. alba* were 1–2% dry mass lower in EAM compared to UAM and control NHM sites (significant oak × treatment interaction effect, Table 1, Fig. 3). Although the main effect of treatments on total phenolics was not significant when tested over the treatment by block interaction (Table 1), when tested over the whole-plot error mean

square, total phenolics were significantly higher in the foliage of trees in UAM sites compared to NHM and EAM sites (treatment effect: $F_{2,4} = 33.96$, $P = 0.0031$; month × treatment: $F_{4,6} = 6.77$, $P = 0.0206$). Treatments did not have a significant effect on understory CT concentrations, nor was there a significant oak by treatment interaction effect for CT levels in the overall model (Table 1).

Trees in different blocks differed in response to logging treatments. In block 1, total phenolics in trees within EAM sites were reduced by 5% dry mass relative to concentrations of trees in NHM and UAM sites. In block 2, trees within UAM and EAM sites had higher levels of total phenolics relative to trees in control sites in May but, in mid-June, trees in

EAM sites had lower concentrations of total phenolics relative to NHM and UAM sites (treatment × block interactions, Table 1, Fig. 4). Differences in concentrations among treatments in block 2 were on the order
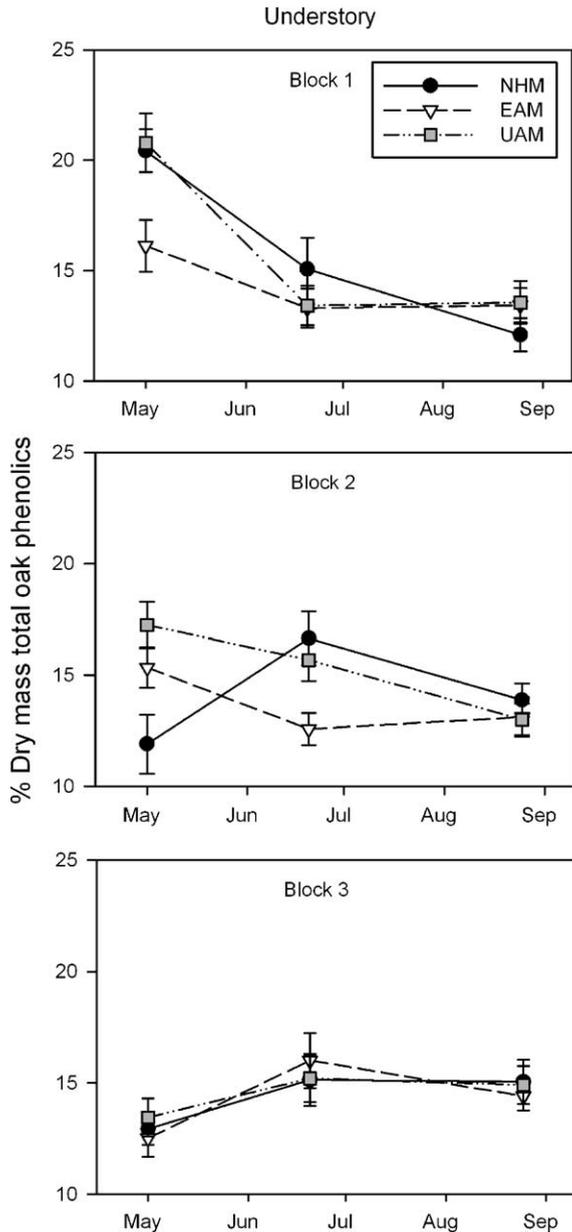

Fig. 4. Mean (±S.E.) percent dry mass total phenolics in understory foliage of trees in NHM, EAM, and UAM treatments in blocks 1–3.

of 4–5% dry mass. Concentrations of total phenolics did not vary among treatments in block 3, and there were no treatment by block interactions for understory CT concentrations.

Although there was no significant main effect of treatment on canopy concentrations of CT or total phenolics, treatments did alter CT concentrations in the second replicate block of our experiment (Fig. 5). Specifically, canopy CT concentrations in *Q. velutina* in block 2 were initially elevated in both logging treatments compared to controls in May, but in June CT concentrations were elevated in trees in UAM but reduced in EAM relative to trees in NHM sites. On the other hand, CT concentrations in *Q. alba* did not differ in May, but were elevated in trees in both UAM and EAM relative to trees on NHM sites in mid- and late-season (treatment × block and M × O × T × B interactions, Table 2, Fig. 5). Differences between mean CT concentrations of trees in logged areas compared to trees in control sites ranged from as little as 3% dry mass decrease (EAM versus NHM, mid-season *Q. velutina*) to a nearly 20% dry mass increase (UAM versus NHM, mid-season *Q. alba*).

4.3. Block effects

Understory foliar phenolics showed spatial variation in concentrations unrelated to treatment differences, as levels of both CT and total phenolics differed among blocks. In mid-June, trees growing in block 3, which represented our youngest forest, had higher levels of CT than trees in blocks 1 and 2 (significant block and month × block effects, Table 1). Total phenolics in understory trees of both species, however, were highest in block 1, intermediate in block 2, and lowest in block 3 in May (significant block and month × block effects, Table 1). Differences among blocks were on the order of 2–4% dry mass for CT and 2–8% dry mass for total phenolics.

Canopy concentrations of CT did not vary significantly among blocks. However, there was a significant oak by block interaction for canopy total phenolics (Table 2): concentrations of total phenolics were greater in the leaves of trees in block 1 for *Q. alba* but greater in trees in block 2 for *Q. velutina*. Differences were only on the order of 1–3% dry mass.
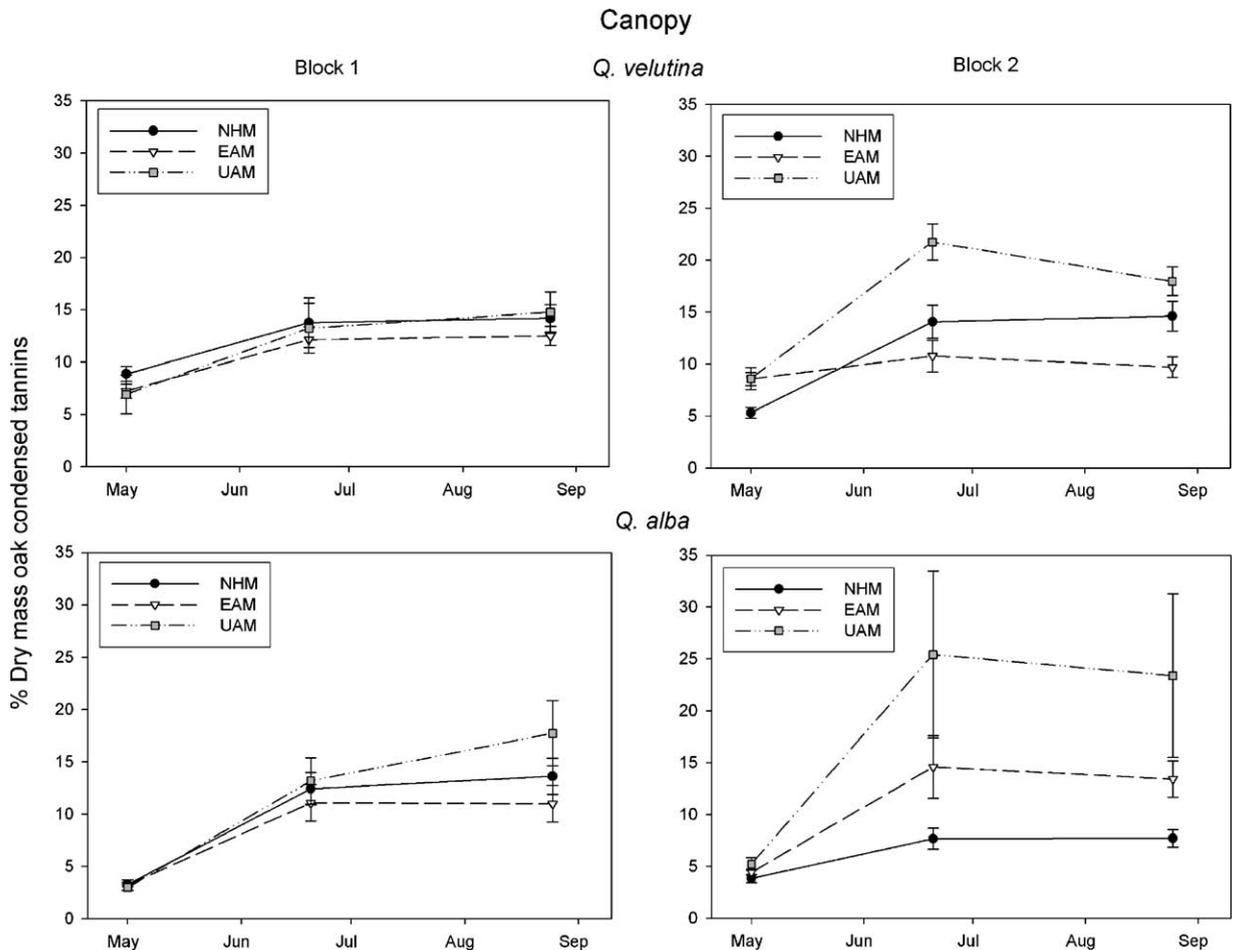
Fig. 5. Mean (±S.E.) percent dry mass condensed tannins in canopy foliage of *Q. velutina* and *Q. alba* trees in NHM, EAM, and UAM treatments in blocks 1 and 2.

4.4. Effects of slope aspect on understory phenolics

Additional spatial variation in phenolics occurred as a result of variation in topography. Concentrations of understory CT and total phenolics were greater at mid-season in trees growing on slopes having south- and west-facing aspects (Table 1, Fig. 6), but did not differ early and late-season (marginally significant month × slope interaction, Table 1). Total phenolics were elevated in trees on south- and west-facing slopes in both mid- and late-season. The amount of variation in phenolics due to slope aspect was low, however, as south- and west-facing slopes had concentrations only 2% dry mass higher.

4.5. Defoliation

The cumulative percentage leaf area removed (% LAR) did not differ among logging treatments for understory *Q. alba* and *Q. velutina* (Table 3), but there was a significant treatment by block interaction. In blocks 1 and 3, defoliation was 2 and 4% higher, respectively, for *Q. alba* and *Q. velutina* trees in UAM compared to NHM and EAM sites, but in block 2, percent LAR was highest for trees in NHM sites. Percent LAR differed significantly among blocks for understory trees: levels of %LAR were 14.4 ± 1.0% in block 1 compared to 18.0 ± 1.0% in blocks 2 and 3. Additionally, understory foliage of *Q.*
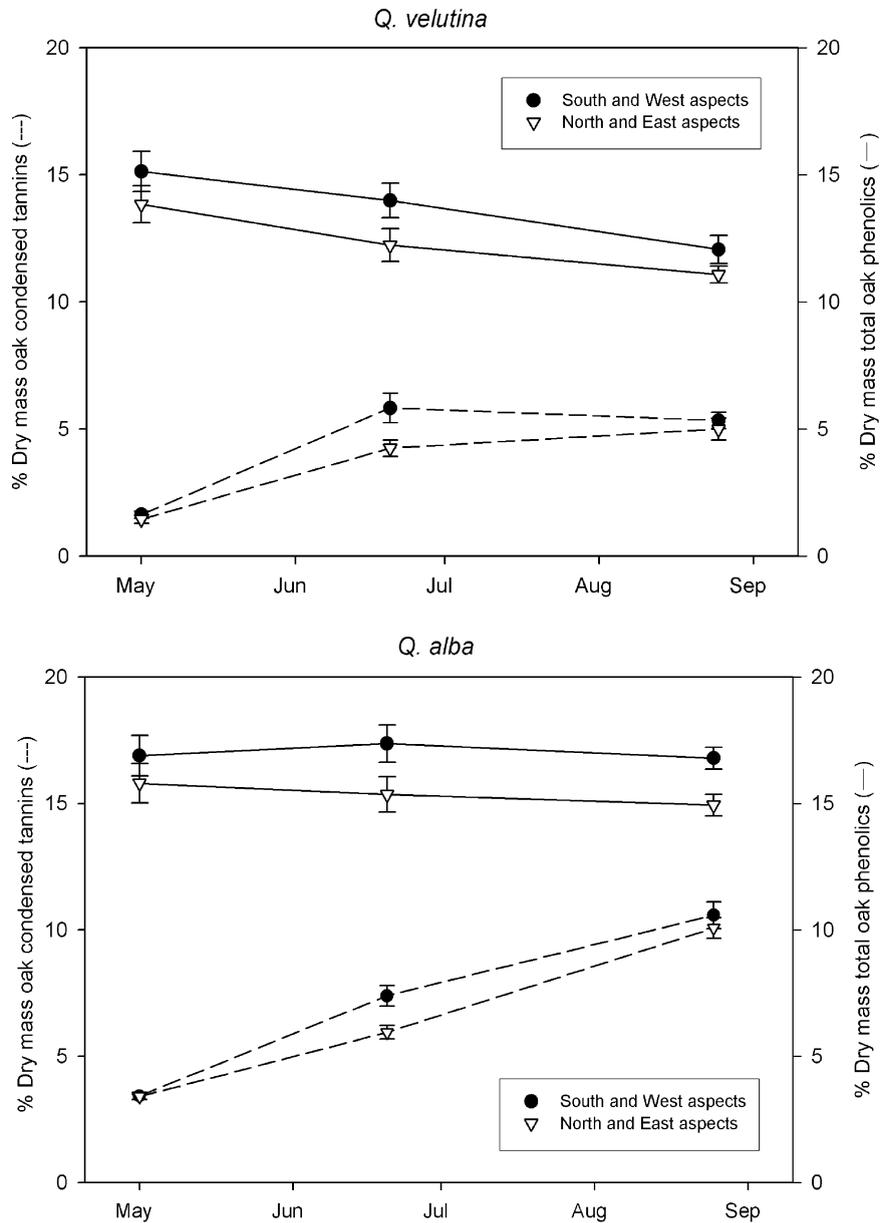
Fig. 6. Mean (±S.E.) percent dry mass oak condensed tannins and total phenolics in understory *Q. velutina* and *Q. alba* on south- and west-facing slopes (ELT 17) and north- and east-facing slopes (ELT 18).

alba and *Q. velutina* growing on slopes having south- and west-facing aspects had lower levels of defoliation (17.8 and 12.4 ± 1.0% LAR, respectively) compared to trees growing on north- and east-facing aspects (20.3 and 17.0 ± 1.0% LAR, respectively, Table 3). Furthermore, there was a significant block by slope

interaction indicating that levels of defoliation on understory trees were greatest in block 2 for ELT 18 (north- and east-facing slopes) but greatest in block 3 for ELT 17 (south- and west-facing slopes). Levels of defoliation in the canopy did not differ among treatments ($F_{2,2} = 1.35$, $P = 0.4252$) or between

Table 3
Results from ANOVA for levels of cumulative defoliation (arcsine square root %LAR) on understory trees in August 2000

Source	MS_{den}	d.f.	F	P
Oak (O)	$MS_{O \times B}$	1	6.63	0.1236
Treatment (T)	$MS_{T \times B}$	2	0.32	0.7451
Block (B)	$MS_{O \times T \times B}$	2	14.76	0.0142
O × T	$MS_{O \times T \times B}$	2	5.01	0.0813
O × B	$MS_{O \times T \times B}$	2	6.93	0.0501
T × B	$MS_{O \times T \times B}$	4	6.99	0.0430
O × T × B (whole-plot error)		4		
Slope (S)	$MS_{Stand(T \times B \times S)}$	1	5.73	0.0287
T × S	$MS_{Stand(T \times B \times S)}$	2	0.20	0.8242
B × S	$MS_{O \times Stand(T \times B \times S)}$	2	5.37	0.0174
O × S	$MS_{O \times Stand(T \times B \times S)}$	1	0.83	0.3768
O × T × S	$MS_{O \times Stand(T \times B \times S)}$	2	0.68	0.5193
O × B × S	$MS_{O \times Stand(T \times B \times S)}$	2	0.97	0.4028
T × B × S	MS_{error}	4	1.78	0.1373
O × T × B × S	MS_{error}	3	0.23	0.8749
Stand (T × B × S)	MS_{error}	18	1.68	0.0500
O × Stand (T × B × S)	MS_{error}	15	0.65	0.8249
Error (split-plot error)		136		

oak species ($F_{1,2} = 2.27$, $P = 0.2706$), but a separate ANOVA indicated that canopy trees had less leaf area removed overall than did understory trees (canopy $11.1 \pm 0.7\%$, understory $16.9 \pm 0.5\%$, $F_{1,228} = 22.32$, $P < 0.0001$).

5. Discussion

We predicted that increased light levels following thinning would result in higher phenolic concentrations in trees in the understory of UAM sites. Our results provide inconsistent support for this prediction. When effects were significant in the understory (in block 1, Fig. 4), trees in UAM sites had concentrations similar to levels in trees in NHM sites. In contrast, when levels in trees in UAM sites were greater than levels in trees in control landscapes (in block 2, Fig. 4), trees in EAM sites also had elevated concentrations. Timber extraction altered canopy phenolics as well, but only in the second block of our experiment. In this block, canopy CT concentrations in *Q. velutina* were elevated in trees in UAM but reduced in EAM relative to trees in NHM sites. Canopy CT concentrations in *Q. alba* were elevated in trees in both UAM and EAM sites relative to trees on NHM sites. Although the results for canopy trees appear consistent with our

predictions, timber extraction did not create large differences in light levels in this stratum, which suggests that other mechanisms may be responsible for observed treatment differences in the canopy.

An alternative pathway by which thinning might influence foliage phenolic levels is through increased soil nutrients and/or decreased plant spacing. Both mechanisms were predicted to reduce levels of phenolics in trees in UAM compared to EAM and NHM sites. Foliar phenolic concentrations were generally higher or no different in UAM trees, however, and the only occasion on which we found lower levels in UAM compared to NHM trees—in mid-season understory *Q. alba* (Fig. 3)—concentrations were reduced in trees in EAM sites as well. Furthermore, block 3 contains approximately 40% fewer large (=4.5 cm dbh) *Q. alba* trees than the other experimental blocks (Kabrick et al., 1997), but not significantly higher phenolic levels (Fig. 4).

The lack of treatment main effects, only significant treatment by block interactions, and results inconsistent with known mechanisms responsible for shifts in phenolics suggest that blocking factors were more important in determining the impacts of logging on phenolics. Evidence available at this time does not suggest that differences in soil type might account for block differences. Our sampling locations generally

occurred on two soil types, Roubidoux sandstone and Upper Gasconade dolomite (Kabrick et al., 2000). Both soil types are described as moderately to very deep, well drained, loamy soils (Kabrick et al., 2000), and the trees we sampled occurred approximately equally on both soil types.

Block differences might reflect underlying differences in forest age, prior land-use history, or plant species composition, rather than differences in soil quality. For example, timber extraction altered understory phenolics in the two older blocks of forest, but not in block 3. All sites were subjected to various amounts of cutting, grazing, and uncontrolled burning prior to acquisition by the Missouri Department of Conservation, but block 3 was the most recently acquired (1952 compared to 1925–1944 for blocks 1 and 2), and thus may be the most strongly affected by previous land-use history and stand age. Preliminary data analysis indicates that concentrations of condensed tannins in *Q. velutina* in May were negatively correlated ($r^2 = 0.30$, $P = 0.0145$, $n = 18$) with stand age, as determined from coring samples of five trees per stand (Shifley et al., 2000). Additional factors not considered, such as temperature (Buse et al., 1998), water (Horner, 1990; Stowe et al., 1994), and microbial activity (Weaver and Heyman, 1997), not only might generate differences in phenolics, but also are likely to interact with changes in soil nutrients and light levels to determine the impacts of timber extraction on foliar phenolics. Future studies of the impact of timber harvest on plant defensive metabolites should sample a wider range of forest types and soil characteristics and should incorporate measures of light levels, soil nutrients, and plant growth or photosynthesis rates.

Significant variation in phenolics due to treatment and block interactions was present early- and mid-season, contrary to our prediction that differences would be expressed late in the growing season. This may be due to the fact that concentrations of total phenolics include both hydrolysable and condensed tannins; hydrolysable tannin concentrations in oaks are often higher and more variable early in the season as leaves expand (Schultz et al., 1982). Furthermore, contrary to our prediction that logging would cause greater changes in levels of understory compared to canopy phenolics, treatment differences were greater in the canopy. Foliar phenolics concentrations in canopy trees in UAM landscapes were as much as

20% dry mass higher, representing a 500% increase relative to canopy trees in control landscapes, whereas understory trees in logged and control areas differed by only 25–60%.

As predicted, response to timber extraction differed between *Q. alba* and *Q. velutina*. Understory *Q. velutina* trees in UAM sites had slightly increased levels of condensed tannins and total phenolics compared to trees in NHM and EAM sites. For *Q. alba*, understory trees generally had lower concentrations in treated landscapes, whereas canopy trees had greater concentrations in treated landscapes. Shure and Wilson (1993) demonstrated that phenolic concentrations in slow and fast growing species responded differently to changes in gap size. Within the genus *Quercus*, *Q. alba* is considered a slower-growing, shade adapted species, whereas *Q. velutina* performs better in gaps and is more drought tolerant (Fowells, 1965). These life-history characteristics are likely to differentially influence resource allocation to growth and defense (Coley, 1983), and may partially explain why we found species-specific differences in the responses of foliar phenolics to timber extraction. Species-specific responses to timber extraction suggest that the degree to which harvest treatment differentially remove oak species or cause changes in subsequent plant species abundances will also impact landscape-level foliar chemistry profiles and host plant quality for herbivores.

An additional consistent pattern was slope-aspect-related variation in phenolics. Understory trees found on slopes having south- and west-facing aspects had consistently higher levels of CT and total phenolics compared to trees on north- and east-facing aspects. While differences were only on the order of 1–4% dry mass, both levels of defoliation (this study) and total insect species richness (Forkner et al., 2004) were lower on slopes having higher levels of polyphenolics. The significant variation in phenolics at the slope-aspect level may represent differentiation due to local adaptation (Sork et al., 1993). In much the same way that agriculturalists include buffers of non-genetically modified plants to prevent insect adaptation to resistant crops, foresters may use data on stand, block, and slope-aspect-related variation in plant anti-herbivore metabolites to manage resources in a manner that prevents large-scale insect outbreaks. In order to maintain pre-existing spatial variation in concentra-

tion of polyphenolics, resource managers should avoid harvesting timber of a single species or from a single ELT. These concerns are particularly important for a generalized herbivore fauna like that found on oaks. Not only do the majority of species that are found to occur on *Q. alba* also feed on *Q. velutina* (Forkner et al., 2004), but they are also found other oak species and non-oak deciduous tree species (Covell, 1984; Marquis et al., in press).

In conclusion, timber extraction affected levels of *Quercus* phenolics. Furthermore, logging-induced changes in canopy trees were much greater than natural spatial variation in phenolic concentrations. Impacts of timber extraction on understory phenolics, on the other hand, were small, and may be so because we are in the first round of cutting and treatments only removed a small amount of timber (10% total timber biomass). Nonetheless, our initial data indicate that insect abundance and species richness (Forkner et al., unpublished data), as well as levels of defoliation (this study) were lower where concentrations of phenolics were higher. Additional data show that densities of some oak herbivores in this system correlate negatively with concentrations of condensed tannins even when levels are less than 5% dry mass (Forkner et al., 2004). Hochwender et al. (2003) showed that even small changes in leaf damage reduce acorn production in *Q. alba* trees in this region. Taken together, these studies suggest that small changes in phenolics resulting from timber harvests may have large consequences for oak herbivore communities. Understory *Q. alba* may show increased susceptibility to insect attack in logged forests (Fig. 3), whereas canopy *Q. alba* may show decreased susceptibility (Fig. 5). On the other hand, *Q. velutina* may show decreased susceptibility to insect attack in both the canopy and understory of selectively logged landscapes (UAM, Figs. 3 and 5). Studies that measure phenolic concentrations over several years would help establish if logging produces persistent changes in phenolics or if treatment effects disappear shortly after timber extraction. Our measurements were conducted 5 years after timber removal, suggesting that treatment-related differences in foliar secondary compounds may persist for several years. Detailed studies with replication across a greater range of forest ages in order to distinguish the effects of timber extraction from spatial variation in phenolics due to forest age or prior management history are needed, as are studies that examine the impacts of logging-induced changes in phenolics on nutrient cycling.

Acknowledgements

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