

Fire effects on insect herbivores in an oak savanna: the role of light and nutrients

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Abstract. 1. Environmental heterogeneity created by prescribed burning provided the context for testing whether the distribution of an oak specialist (the lace bug, *Corythuca arcuata*) could be explained by stoichiometric mismatches between herbivore and host plant composition.

2. Field observations showed that lace bug density was seven-fold higher in frequently burned than in unburned units.

3. Lace bug density did not increase with leaf nutrient concentrations, but was instead associated with higher light levels, higher concentrations of leaf carbon (C), lignin and total phenolics, and lower levels of cellulose. In addition, lace bugs reared on high-light leaves had higher levels of survivorship than those fed on low-light leaves.

4. Sampling restricted to full-sun leaves was used to test whether fire-related changes in leaf nitrogen (N) and phosphorus (P) concentrations have a secondary influence on lace bug success. This sampling provided only limited evidence for nutrient limitation, as decreases in leaf N and P were associated with an increase in lace bug mass but a decrease in density.

5. It is concluded that burning probably promotes lace bug population growth by increasing canopy openness, light penetration, and the availability of C-based metabolites, and thus simple stoichiometric mismatches between herbivores and host plants are not of primary importance in this system.

Key words. Body size, carbon quality, ecological stoichiometry, herbivory, leaf chemistry, nitrogen, phosphorus, plant–insect interactions, *Quercus*.

Introduction

Variation in the chemical composition of plants often significantly affects the success of individual herbivores (Awmack & Leather, 2002) and the distribution and local abundance of herbivore populations (Mattson, 1980; White, 1993). Chemical features influencing plant quality for herbivores include water content, concentrations of secondary metabolites, and levels of nitrogen (N) and other nutrient correlates. However, there is growing awareness that the ecological relevance of variation in nutrient content depends not only on the intrinsic properties of leaves but also on the mismatch between leaf composition and the nutritional demands of herbivores (Elser *et al.*, 2000; Fagan &

Denno, 2004). Ecological stoichiometry, the study of element balance in living systems, provides a framework for linking trophic imbalances driven by variation in food quality to the physiological traits of organisms that generate population-level patterns (Sturner & Elser, 2002).

Much evidence suggests that N content determines plant nutritional quality for a wide range of terrestrial insect herbivores (White, 1993). For example, N levels in foliage are usually more than an order of magnitude less than levels in insect tissue (Mattson, 1980) and higher N availability often increases development rate and survival for insect herbivores (Hunter & McNeil, 1997; Joern & Behmer, 1997). As a result, N availability is predicted generally to limit the spatial distributions and population growth rates of insect herbivores – the N limitation hypothesis (White, 1993). Although rarely considered, other nutrients such as phosphorus (P) may also affect the population

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dynamics of terrestrial insects because of the large disparity between insect P demands and the supply of P in plant tissue (Sternner & Elser, 2002). For example, Schade *et al.* (2003) suggested P availability limits population growth for desert weevils, which were more abundant on host plants with foliage rich in P. Carbon (C)-based compounds without N or P, such as sugars and starch, are essential components of insect diets (Dadd, 1985) and thus could potentially also limit insect herbivore populations. However, higher concentrations of these compounds in plant tissue often reduce herbivore success by diluting access to other nutrients (e.g. Clancy, 1992; Whittaker, 1999) (but note Goverde *et al.*, 1999).

In this study, we examine how population- and individual-level traits of an insect herbivore, the lace bug *Corythuca arcuata*, vary among oak trees subjected to various frequencies of prescribed burning over the past 39 years. The prescribed burning experiment occurs in a 300-ha area of the Cedar Creek Natural History Area (hereafter, Cedar Creek) located in central Minnesota. Plots have been subjected to experimental fires at frequencies ranging from nearly annual burns to complete fire exclusion (Reich *et al.*, 2001).

Fire can lead to modifications in vegetation physiology that affect herbivore performance (Rieske, 2002; Adams & Rieske, 2003). Fire can result in a short-term increase in leaf N concentrations (Kruger & Reich, 1997), which may reflect increases in soil N availability following ash deposition or changes in root : leaf ratios in post-burn vegetation (Reich *et al.*, 1990). Over longer periods, fire can reduce soil N availability as a result of volatilisation and leaching (Raison, 1979; Ojima *et al.*, 1994; Dijkstra *et al.*, 2006), which in turn can lead to changes in plant species composition and lower leaf N concentrations. However, at the sites studied here, Reich *et al.* (2001) found in a community-level comparison that green leaf N concentration in oaks did not vary with fire frequency. Less is known about how fire affects P availability for herbivores. Because phosphate does not volatilise in low intensity burns, P deposition in ash may increase soil P availability (Kaufman *et al.*, 1994), potentially affecting leaf P concentrations. Fire can also affect leaf quality as a result of changes in access to light for surviving vegetation. Longterm burning at our site is associated with a change in vegetation structure from domination by woody species in unburned plots to low tree cover and abundant herbaceous vegetation in frequently burned plots (Peterson & Reich, 2001). These differences are related to increases in canopy openness (Reich *et al.*, 2001), which are likely to change light availability for oaks. Increased light availability can potentially reduce leaf quality for herbivores by diluting N and P concentrations, and by inducing accumulation of secondary metabolites, such as phenolics (Dudt & Shure, 1994), and digestibility reducers, such as cellulose and lignin (Niinemets & Kull, 1998).

Our study had three components. Firstly, we tested whether the burning regime affected lace bug abundance and whether lace bug presence and density were related to light availability and leaf chemistry. Secondly, we compared the body size and local abundance of adult lace bugs on trees that were exposed to different burning regimes but experienced similar light conditions. Standardising light availability allowed us to isolate the

importance of fire-related variation in nutrient availability. Specifically, we tested whether lace bug body size and abundance were positively related to foliar N and P levels in full-sun leaves. Finally, we tested whether leaves from different light environments differentially supported lace bug development under controlled laboratory conditions to determine whether abundance patterns in the field could result from variation in leaf quality among sites.

Materials and methods

The prescribed burning experiment at Cedar Creek began in 1964. Burns are conducted in April or May, before leaf emergence on oaks. Fires are generally of low intensity (Reich *et al.*, 2001). The frequency of experimental burns in units ranges from nearly annual fires to complete fire exclusion. Units range in size from 2.4 ha to 30 ha. Two species of oak (bur oak, *Quercus macrocarpa*, and northern pin oak, *Quercus ellipsoidalis*) are the dominant tree species in this site, particularly in frequently burned units. Bur oaks generally increase in abundance relative to northern pin oaks in more frequently burned units (Peterson & Reich, 2001).

Corythuca arcuata is a specialist on bur oaks (at least at this site) and occurs across the burn frequency gradient. Adults oviposit on leaves in late May to early June and both nymphs and adults feed on leaf mesophyll during the rest of the growing season. Their feeding activity results in widespread leaf discoloration and mottling. They are relatively immobile; adults have functional wings but are reluctant fliers, even when vigorously disturbed (A.D.K., personal observation).

In the first component, we measured lace bug abundance and leaf traits across the full range of light and nutrient conditions created by burning. For this component, we collected leaves and insects in three units that had never been burned experimentally (unburned) and three that had been burned 0.9 times per year during the experimental period (high burn). Burning in one high-burn plot was initiated in 1995; treatments in other plots began in 1964. We sampled trees in mid-July along single transects within each unit. Each transect extended at least 150 m across a unit; entry points at a unit's border were chosen randomly, and transect orientation was chosen randomly within ± 45 degrees of the perpendicular to the border. Along each transect, bur oak trees were sampled if they fell within 10 m of the transect and were at least 10 m from other sampled trees. We sampled four branches from each of 10 trees in each unit. We sampled leaves from a ladder, which allowed us to access leaves within about 6 m of the ground but not the uppermost portion of the canopy (~ 8 –15 m). On each branch, we counted the number of lace bug adults and eggs on 100 leaves, moving inward from the branch tip. Lace bugs deposit eggs on leaves in clutches. We categorised clutch sizes as small (10–50 eggs), medium (50–250 eggs), or large (250–500 eggs). We also collected five leaves from each branch for chemical analyses. We measured light availability at each branch using a Li-cor LI-250 light meter (LI-COR Biosciences, Lincoln, NE, USA). At each branch, light availability was measured three times on cloud-free days: in the morning (09.00–11.00 hours), early afternoon (13.00–15.00 hours), and late afternoon (15.00–17.00 hours). We

estimated the proportion of light received by comparing measurements at branches with periodic measurements taken in areas receiving full sun. We defined light availability at a branch as the average of the three measurements.

We dried isolated leaves and insects at 60 °C for 48 h. After drying, we ground leaves to powder in a ball mill (SPEX Certiprep, Metuchen, NJ, U.S.A.), then analysed subsamples for P, C, N, glucose, starch, phenolics, hemicellulose, cellulose, and lignin. We measured P concentration in subsamples using persulphate acid digestion and ascorbate-molybdate colorimetry on an ALPKEM FS3000 autoanalyser (OI Analytical, College Station, TX, U.S.A.), and C and N concentrations using a Perkin-Elmer 2400 CHN analyser (Perkin-Elmer Life and Analytical Sciences, Inc., Waltham, MA, USA). Glucose concentration was determined by colorimetry after ethanol extractants were combined with phenol and concentrated sulphuric acid. This technique was also used to quantify starch after it had been isolated from the ethanol insoluble pellet and hydrolysed with amyloglucosidase in an acetate buffer. Total phenolic concentration was determined using a modification of the Price and Butler method, which involves colorimetry after combining samples with potassium ferricyanide, anhydrous ferric chloride and a phosphoric acid–gum arabic stabiliser (Graham, 1992). Using an Ankom 200 fibre analyser (Ankom Technology, Macedon, NY, U.S.A.), we determined hemicellulose as the fraction soluble in 1 N H₂SO₄ detergent but insoluble in neutral detergent, cellulose as the fraction soluble in concentrated H₂SO₄ but insoluble in 1 N H₂SO₄ or neutral detergent, and lignin as the acid-insoluble fraction (Van Soest, 1994).

In the second component, we compared lace bug adult mass and local abundance on full-sun leaves across the burn gradient to focus on effects of fire-related changes in nutrient availability. For this work, we collected leaves and insects in three unburned, three medium-burn (burned 0.33–0.5 times per year), and three high-burn units. Within each unit we selected three sites (hereafter, gaps) which contained at least two bur oak trees; gaps in unburned units were true gaps in an otherwise closed canopy, whereas gaps in burned units were areas at the margins of clusters of pin and bur oak. We standardised light conditions across gaps by sampling only leaves receiving full sun from at least late morning (11.00 hours) to mid-afternoon (15.00 hours) during the sampling period. We collected samples in early August. At each of two to three canopy trees per gap, we surveyed 100 leaves and collected the five on which we estimated lace bug abundance was highest. We used the number of adults on these leaves as a measure of local abundance. Samples were stored in a freezer until the number of individual insects per sample was counted. We analysed leaves for P, C, and N as described above and determined dry mass in three to six insects per tree using an electronic balance ($\pm 0.1 \mu\text{g}$).

We also examined the development of lace bug nymphs on host leaves under laboratory conditions. This work allowed us to isolate the effect of leaf quality on lace bug performance from other environmental factors associated with variation in light availability and burn treatment. Two replicate leaf clusters (sprigs with two to three leaves) were collected from four trees in each of three conditions: low-light conditions ($3.8 \pm 0.9\%$ maximum available, mean \pm standard error, SE)

in unburned plots, high-light conditions ($66.0 \pm 5.9\%$) in unburned plots, and high-light conditions ($70.5 \pm 7.3\%$) in burned plots. Leaves were maintained in waterpiks within larger containers, and kept in a growth chamber with 16 : 8 h light : dark and 28–20 °C temperature schedules. We initially placed 10 second to third instar lace bug nymphs on each leaf cluster. Nymphs for the experiment were collected from a single, medium-burn unit in late July. Every 3 days, experimental nymphs were gently transferred with soft forceps to fresh leaves from the same tree. We recorded adult emergence and nymph mortality each day. Individuals that were unaccounted for (8.4%) were excluded from analysis. We ended the experiment after 11 days, when all bugs had either died or emerged as adults.

All statistical analyses were performed with the Systat 11 statistical package (Systat Software Inc., San Jose, CA, USA). In the first component, we compared lace bug abundance, light availability, and leaf chemistry to burn treatment using nested analysis of variance (ANOVA), with tree-of-origin nested within unit. Dependent variables were mean values for trees. Light availability data were arcsine-transformed for analysis; abundance and leaf chemistry values were log-transformed. Note that the scale of the longterm burning experiment means that the level of replication within treatment ($n = 2$) is limited. Thus, our nested ANOVA analyses may be unable to identify all actual effects of burn treatment.

We also conducted regression analyses to investigate possible reasons for treatment effects on lace bugs via associations with light and leaf chemistry. Across all trees in the survey, we used linear regression analyses with abundance of lace bug adults or eggs (analysed separately) as dependent variables. For leaf chemistry, we used multiple regression with a backward stepwise process that removes the variables with the highest *P*-values until only those with $P < 0.1$ remain in the model. Independent variables were leaf N, P, C, glucose, starch, hemicellulose, cellulose, lignin, and total phenolics. We also assessed how lace bug abundance was associated with light availability and leaf chemistry among trees within burn treatments. Because lace bugs were not found on many trees in unburned areas, we used logistic regression analyses with lace bug presence or absence on trees as the dependent variable in within-treatment comparisons. For the leaf chemistry analysis, the backward stepwise process and identity of independent variables were the same as described above for linear regression analyses.

In the second component, we sampled full-sun areas and compared lace bug dry mass, abundance, and leaf N and P concentrations among burn treatments using nested ANOVA. Here, dependent variables were mean values for gaps, and gaps were nested within unit in the analysis. To investigate possible reasons for burn treatment effects, we also compared lace bug mass and abundance with N and P in full-sun leaves using multiple linear regression analyses (as described above).

In the laboratory rearing experiment, we used nested ANOVA to compare among treatments the (arcsine-transformed) proportion of lace bugs surviving to adulthood. In this analysis, source branch for leaves was nested within tree. Throughout, pairwise comparisons were made with Tukey's HSD (honestly significant differences) tests.

Results

Effects of light availability

Transect sampling revealed that lace bugs were significantly more abundant in frequently burned units than in unburned units (Fig. 1; adults: $F_{1,4} = 28.167$, $P = 0.006$; eggs: $F_{1,4} = 55.271$, $P = 0.002$). In frequently burned units, 74% of 120 branches sampled had adults on them and 83% of branches showed evidence of lace bug oviposition. By contrast, adult lace bugs were present on only 16% of the 120 branches sampled in unburned units, and only 17% of branches had egg clutches. The difference in lace bug abundance between burned and unburned units corresponded to differences in light availability and leaf chemistry. Light availability at branches was significantly and substantially higher in burned units than in unburned units ($F_{1,4} = 25.804$, $P = 0.007$). Leaves from burned units had lower concentrations of N and P and higher concentrations of total phenolics than those from unburned units, but they also had significantly higher starch concentrations and lower levels of hemicellulose and cellulose (Table 1). Across all trees, lace bug abundance increased with light availability (adults: $r^2 = 0.370$, $P < 0.001$; eggs $r^2 = 0.421$, $P < 0.001$). In addition, multiple regression analysis indicated that adult abundance increased with leaf C ($\beta \pm SE = 18.075 \pm 5.707$, $P = 0.003$) and decreased with leaf N ($\beta \pm SE = -2.397 \pm 0.306$, $P < 0.001$) and cellulose ($\beta \pm SE = -2.056 \pm 0.853$, $P = 0.019$), whereas egg abundance was significantly (negatively) associated with lignin ($\beta \pm SE = -3.890 \pm 1.559$, $P = 0.016$) and cellulose ($\beta \pm SE = -10.149 \pm 2.735$, $P < 0.001$), and positively associated with total phenolics ($\beta \pm SE = 2.566 \pm 0.595$, $P < 0.001$).

Lace bug distribution was also related to light availability and corresponding changes in leaf chemistry within unburned units. Logistic regression analyses indicated that trees with lace bugs received more light than trees without lace bugs (Fig. 2; adults: $\beta \pm SE = 2.779 \pm 1.326$, $P = 0.036$; eggs: $\beta \pm SE = 3.354 \pm 1.460$, $P = 0.022$). In addition, leaves in unburned units with lace bug eggs contained significantly more starch ($\beta \pm SE = 2.664 \pm 10.461$, $P = 0.048$) and lignin ($\beta \pm SE = 2.664 \pm 10.461$, $P = 0.048$) than those without eggs (Fig. 3); a difference in total phenolics was almost significant ($\beta \pm SE = 15.360 \pm 7.903$, $P = 0.052$). By contrast, light availability varied little among trees in burned units, and neither egg presence ($\beta \pm SE = 1.869 \pm 1.361$, $P = 0.170$) nor adult presence ($\beta \pm SE = -0.905 \pm 1.213$, $P = 0.455$) were significantly related to light availability in these units (Fig. 2). Multiple logistic regression revealed that leaves in burned units with eggs or adults on them did not differ from leaves without lace bugs in any measured chemical component (Fig. 3).

Effects of nutrient availability

Dry mass and abundance of adult lace bugs on full-sun leaves differed significantly among locations. Adult mass differed significantly among burn treatments ($F_{2,6} = 5.285$, $P = 0.047$) and was highest in unburned plots (Fig. 4). Overall, adult mass var-

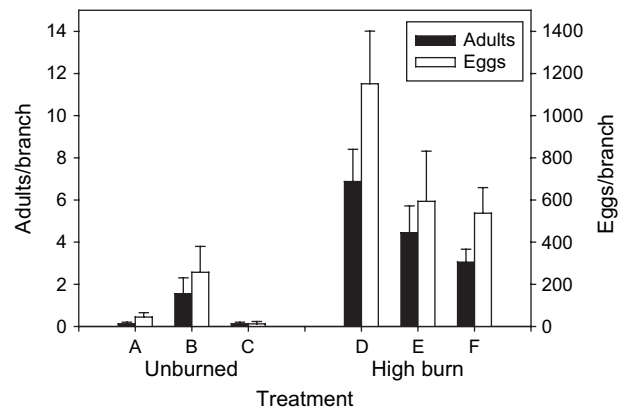


Fig. 1. Lace bug abundance (mean + 1 standard error) on trees in unburned and frequently burned units. Units are labelled A–F. Abundance is the number of lace bugs on a branch containing 100 leaves. Egg numbers were estimated by sorting clutches into size classes (small, medium, large) and using the median value for each class (30, 150, 375) times the number of clutches in that class.

ied more than two-fold among sampling locations. Abundance on full-sun leaves also differed among burn treatments ($F_{2,6} = 5.285$, $P = 0.047$), but was lowest in unburned areas (Fig. 4).

There was also significant variation among locations in N and P concentrations in full-sun leaves (Fig. 4). Leaf N differed significantly among burn treatments ($F_{2,6} = 6.885$, $P = 0.028$) and was highest in unburned plots, whereas leaf P differed significantly among units ($F_{6,14} = 5.643$, $P = 0.003$), but not among burn treatments ($F_{2,6} = 0.791$, $P = 0.495$). Across all gaps, multiple regression analyses showed adult mass increased with P concentration ($\beta \pm SE = 0.673 \pm 0.109$, $P < 0.001$) and adult abundance decreased with N concentration ($\beta \pm SE = -2.603 \pm 0.891$, $P = 0.008$) in full-sun leaves.

Survivorship experiment

Under controlled conditions in the laboratory, survivorship varied significantly among lace bugs reared on different leaf types ($F_{2,9} = 13.20$, $P < 0.001$). Survival to adulthood was higher on high-light leaves from unburned units (mean per replicate group $\pm SE = 75.4 \pm 7.2\%$) than on either shade leaves from unburned units ($42.2 \pm 6.9\%$) or on high-light leaves from burned units ($56.5 \pm 7.7\%$).

Discussion

The effects of fire on plant communities are well documented, but less is known about how burning influences insect herbivore populations (Warren *et al.*, 1987; Swengel, 2001; Knight & Holt, 2005). Here, we show that densities of lace bugs, a specialist on bur oak, were more than seven times higher on trees in frequently burned units than on those in unburned units (Fig. 1), and their presence was associated

Table 1. Dependence of leaf chemical traits on burn treatment, analysed with separate nested ANOVAs for each trait.

Variable	Mean \pm 1 standard error		$F_{1,4}$	P
	Unburned units	Burned units		
Nitrogen, % dry mass	2.71 \pm 0.13	2.18 \pm 0.13	8.67	0.042
Phosphorus, % dry mass	0.22 \pm 0.01	0.18 \pm 0.01	15.06	0.017
Carbon, % dry mass	47.55 \pm 0.30	48.13 \pm 0.20	2.80	0.169
Glucose, % dry mass	8.19 \pm 0.91	9.44 \pm 0.18	1.20	0.335
Starch, % dry mass	2.99 \pm 0.18	5.55 \pm 0.25	59.18	0.002
Hemicellulose, % dry mass	18.21 \pm 0.28	15.50 \pm 0.52	27.59	0.006
Cellulose, % dry mass	16.49 \pm 0.30	14.74 \pm 0.14	1.33	0.313
Lignin, % dry mass	10.84 \pm 0.47	10.17 \pm 0.34	20.86	0.010
Total phenolics, GAE/dry mass	63.20 \pm 11.59	120.81 \pm 2.56	20.83	0.010

GAE, gallic acid equivalents.

with higher light levels, changes in leaf C quality and reductions in leaf N concentration. These results suggest that fire effects on vegetation structure have a more important influence on lace bug distribution than burn-related changes in nutrient availability.

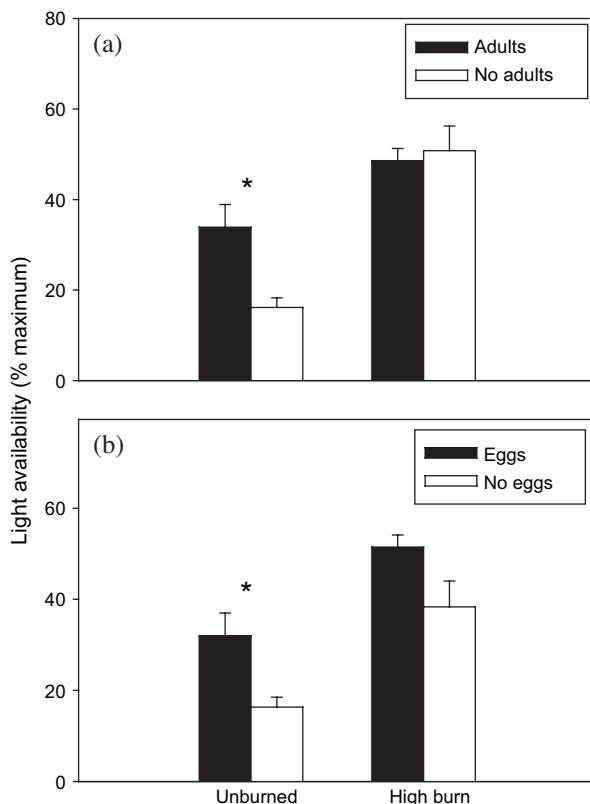


Fig. 2. Light availability (% maximum available, mean \pm 1 standard error) at trees with and without lace bug adults (a) and eggs (b) in unburned and frequently burned units. * indicates a significant relationship between lace bug presence and light availability in logistic regression analysis.

Longterm burning at Cedar Creek, our study site, has caused significant changes in factors that are likely to be relevant to insect herbivores, including a reduction in soil N availability, an increase in canopy openness, and changes in plant community composition (Reich *et al.*, 2001). Despite these changes, Siemann *et al.* (1997) found no significant relationship between burn treatment and abundance in over 500 insect species collected at Cedar Creek (their survey did not include lace bugs). The marked response of lace bugs to frequent burning may thus be exceptional, but it is likely to have important community-level implications because of the high density and widespread distribution of these insects on a dominant tree species at this site.

Differences in lace bug abundance between frequently burned and unburned units reflected large differences in light availability; similarly, in unburned units, branches with lace bugs received more light than branches without lace bugs (Fig. 2). Frequent fire is an important factor limiting dominance by trees in savanna plant communities (Anderson *et al.*, 1999; Peterson & Reich, 2001): at Cedar Creek, the percentage of woody canopy openness is on average three-fold higher in frequently burned units than in unburned units (Reich *et al.*, 2001). Bur oaks occur across the range of burn treatments at this site. However, in unburned areas they are in the under-storey of a closed canopy or at the margins of gaps, whereas, in burned areas, individual trees are generally widely spaced in a savanna landscape (Peterson & Reich, 2001). Mortality in bur oaks decreases with increasing fire frequency at this site, probably because of their intolerance of shading and their ability to survive low-intensity fires with little damage; as a result, the relative abundance of bur oaks is higher in frequently burned units (Peterson & Reich, 2001). The widespread occurrence of lace bugs in burned units, their scarcity in unburned units, and the visible leaf scarring resulting from lace bug feeding suggest that these insects may dampen the positive effect of fire on bur oak dominance in this system.

Lace bug distribution also corresponded to differences in leaf chemistry associated with light availability. Burning was associated with substantial changes in the relative concentrations of leaf C constituents: leaves in frequently burned units had less

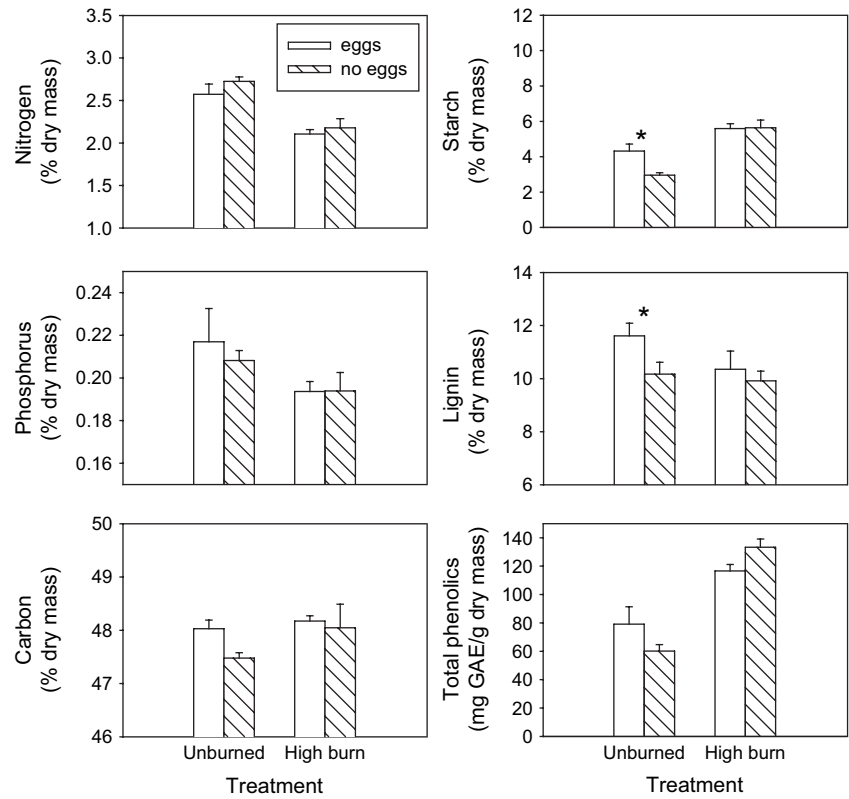


Fig. 3. Mean (+1 standard error) concentrations (% dry mass) of elements (nitrogen, phosphorus, carbon), soluble carbohydrates (glucose, starch), lignin, and total phenolics in leaves with and without lace bug eggs in unburned and frequently burned units. Phenolics are reported as gallic acid equivalents (GAE). * indicates a significant relationship between lace bug presence and light availability in logistic regression analysis.

structural components (hemicellulose and lignin), substantially more starch, and more total phenolics (Table 1). Similarly, lace bug presence in unburned areas was significantly (positively) associated with leaf starch, and a positive association with phenolics was almost significant. Differences in leaf C constituents

are likely to affect leaf palatability for lace bugs. Complex polysaccharides such as hemicellulose and cellulose may impede access to target tissue for piercing insects such as lace bugs, and starch is a potential metabolic substrate. Phenolics such as tannins have been implicated as anti-herbivore agents

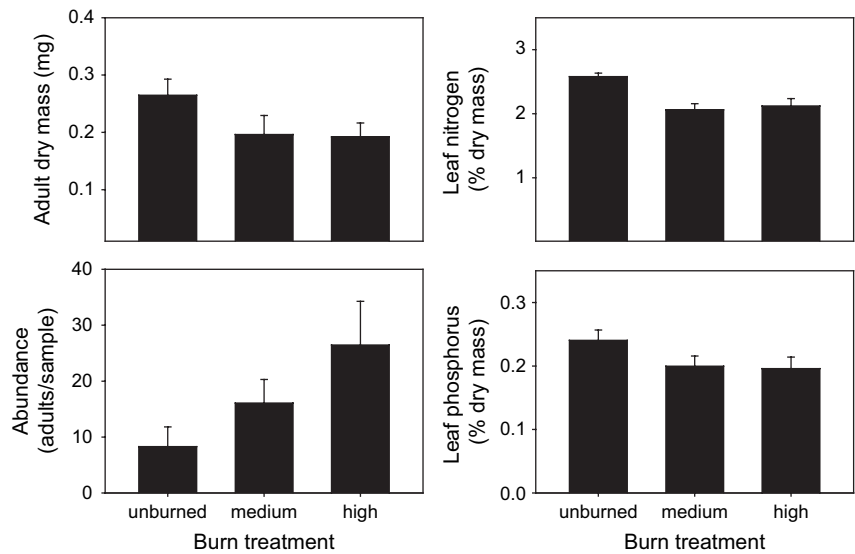


Fig. 4. Lace bug dry mass and abundance, and oak leaf phosphorus and nitrogen concentrations (% dry mass) from full-sun locations in different burn treatments. Bars represent means + 1 standard error. Error bars represent variation among burn units. Nested ANOVAs indicate significant differences among treatments for each independent variable.

(Feeny, 1970), making it somewhat surprising that lace bug presence was associated with higher leaf phenolic concentrations. However, it is now clear that phenolics are a heterogeneous collection of compounds with multiple functions, only some of which have detrimental effects on insect herbivores (Close & MacArthur, 2002; Heil *et al.*, 2002). In addition, because of corresponding changes in other leaf constituents, such as starch, it is not possible from our results to determine if phenolics negatively affect leaf quality for lace bugs. More generally, the multiple changes in leaf chemistry clearly indicate that the ecological relevance of variation in secondary metabolite concentrations is difficult to assess without experimental manipulation of leaf quality (Forkner *et al.*, 2004). Under controlled conditions, lace bugs reared on high-light leaves from unburned areas were more likely to survive to adulthood than those fed on low-light leaves, suggesting that variation in leaf chemistry may support the relationship between light availability and the distribution of lace bugs in the field.

The role of nutrients is less clear than the role of light. Across the full range of light conditions, lace bug abundance was negatively related to leaf N concentration. These results suggest that simple stoichiometric constraints are not of primary importance in this system. However, nutrient levels may play a role when light availability is sufficiently high. On full-sun leaves, lace bug adult mass varied substantially among locations and was positively associated with an increase in leaf P concentration. Higher diet quality often leads to faster growth rates and larger adult size in insects (Nylin & Gotthard, 1998) and thus lace bugs may have been larger on nutrient-rich leaves in full sun because they provided enough high-quality substrate to support rapid growth. In addition, under controlled conditions lace bugs had higher survivorship on high-light leaves from nutrient-rich unburned areas than on high-light leaves from frequently burned areas. The importance of leaf nutrient concentrations remains unresolved, however, because lace bug abundance on full-sun leaves decreased significantly with leaf N concentration. One possible explanation for the larger adult mass but lower density on full-sun, nutrient-rich leaves is that local populations on these leaves are regulated by other factors such as predation or dispersal constraints; limited access to nutrient-rich gaps within densely forested, unburned areas is particularly likely for these reluctant fliers.

The great value in ecological stoichiometry lies in its simple parameterisation of complex ecological processes. By describing organismal biochemistry in terms of element ratios, ecological stoichiometry provides a framework for linking the physiological properties of organisms to the cycling of nutrients in ecosystems. However, it is still unclear under what circumstances element concentrations will sufficiently describe the demands of consumers and the characteristics of foods that guide trophic interactions (Anderson *et al.*, 2004). Our results suggest that neither N nor P availability determine lace bug distribution, and that the relative quantity of different C-based compounds, rather than the concentration of C, is the salient characteristic of leaves for lace bugs. It is possible that consideration of higher-order biochemistry may be generally important for understanding plant–herbivore dynamics driven by light availability.

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