

LONG-TERM BURNING INTERACTS WITH HERBIVORY TO SLOW DECOMPOSITION

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Abstract. Fires can generate spatial variation in trophic interactions such as insect herbivory. If trophic interactions mediated by fire influence nutrient cycling, they could feed back on the more immediate consequences of fire on nutrient dynamics. Here we consider herbivore-induced effects on oak litter quality and decomposition within a long-term manipulation of fire frequency in central Minnesota, USA. We focused on bur oak (*Quercus macrocarpa*) trees, which are common across the fire frequency gradient and are often heavily infested with either lace bugs (*Corythuca arcuata*) or aphids (*Hoplochaitropsus quercicola*). We used targeted exclusion to test for herbivore-specific effects on litter chemistry and subsequent decomposition rates. Lace bug exclusion led to lower lignin concentrations in litterfall and subsequently accelerated decomposition. In contrast, aphid exclusion had no effect on litterfall chemistry or on decomposition rate, despite heavy infestation levels. Effects of lace bug herbivory on litterfall chemistry and decomposition were similar in burned and unburned areas. However, lace bug herbivory was much more common in burned than in unburned areas, whereas aphid herbivory was more common in unburned areas. These results suggest that frequent fires promote oak–herbivore interactions that decelerate decomposition. This effect should amplify other influences of fire that slow nitrogen cycling.

Key words: afterlife effects; aphid herbivory; *Corythuca arcuata*; decomposition; fire; lace bug herbivory; *Hoplochaitropsus quercicola*; lignin; nitrogen cycling; oak savanna; phenolics; *Quercus macrocarpa*.

INTRODUCTION

Fires can cause major disturbances to ecosystem-level processes through predictable changes in abiotic and biotic environments (Kozłowski and Ahlgren 1974, Boehner 1982, Tilman et al. 2000, Wan et al. 2001). Direct effects of fire result from nutrient volatilization, conversion of organic biomass and detritus into ash, and microclimate alterations (Ojima et al. 1994), and more indirect effects stem from changes in below- and aboveground communities (Hart et al. 2005). Fire-related changes in the composition of plant communities are well documented, but fire can also affect the distribution and abundance of species at higher trophic levels (Warren et al. 1987, Swengel 2001) and in turn the nature, strength, and spatial patterning of trophic interactions (Knight and Holt 2005, Kay et al. 2007). Little is known, however, about how fire mediates trophic interactions that affect nutrient cycling and how such effects amplify or damp more immediate consequences of fire.

In this study, we examine how fire interacts with insect herbivory to affect litter decomposition rates. Insect herbivory can alter nutrient flux from aboveground to

belowground systems via several pathways (Bardgett and Wardle 2003, Schowalter 2006) including additions of frass and carcasses (Frost and Hunter 2004) and changes in the quantity and chemistry of litter inputs (Hunter 2001). Changes in litter chemistry can occur when herbivores disproportionately remove high-quality forage (Ritchie et al. 1998, de Mazancourt and Loreau 2000) or, more directly, through herbivore-induced changes in the nutrient or secondary chemical composition of infested plants that carry over to the litter. This “afterlife” effect has received relatively little attention, but recent work suggests it may be common and strong enough to significantly influence nutrient dynamics (Chapman et al. 2003, 2006, Schweitzer et al. 2005).

Herbivore-induced changes in litter chemistry can have diverse but predictable effects on decomposition rate. Chapman et al. (2006) hypothesized that changes are specific to tree life form: insect herbivory leads to accelerated decomposition of evergreen litterfall because of premature leaf abscission, and to decelerated decomposition of deciduous litterfall because of induction of secondary compounds. Induced changes can also vary within plant species across genotypes that differ in susceptibility to herbivory (Chapman et al. 2003, Schweitzer et al. 2005).

Other factors may also influence the size of afterlife effects. For example, herbivore effects on litterfall chemistry likely vary across environmental gradients

Manuscript received 3 October 2007; revised 29 November 2007; accepted 11 December 2007. Corresponding Editor: M. A. Arthur.

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because induction of defensive compounds is often sensitive to resource conditions (Chapin et al. 1987, Hunter and Schultz 1995). Afterlife effects may also depend on herbivore type because specific plant defenses can be elicited by cues from particular herbivores (Hartley and Lawton 1991, Karban and Baldwin 1997). For example, Hartley and Lawton (1987) found folivory by caterpillars induced higher phenolic levels in birch leaves than did attack by leaf-mining beetles. If distinct plant responses to particular herbivores lead to differences in litterfall quality, local patterns of nutrient dynamics may depend on the identity of abundant herbivores.

Here, we tested two hypotheses examining the interaction between fire and herbivory on decomposition: the environmental condition hypothesis, which posits that fire-related changes in resources (e.g., soil nutrients) affect the impact of herbivory on litterfall chemistry, and the herbivore identity hypothesis, which posits that fire affects the relative impacts of herbivores with different effects on litterfall chemistry. We tested these hypotheses using a targeted exclusion experiment and an herbivory survey.

Our study site in the Cedar Creek Natural History Area (CCHNA) in central Minnesota, USA has been subject to an experimental gradient in fire frequency since 1964 (Reich et al. 2001). We focused on bur oak (*Quercus macrocarpa*), a dominant tree species at this site, and its two principal herbivores: a lace bug (*Corythuca arcuata*) and an aphid (*Hoplochaitropsus quercicola*). Lace bugs are found across the burn frequency gradient, whereas aphids are only common in unburned areas. Bur oaks tend to be heavily infested with either lace bugs or aphids, rarely both. We tested the environmental condition hypothesis by assessing whether effects of lace bug herbivory on decomposition were similar in burned and unburned areas. We tested the herbivore identity hypothesis by examining whether lace bug and aphid herbivory differentially affected litterfall chemistry and decay rate in unburned areas (where both species are common), and by comparing lace bug and aphid herbivory levels in burned and unburned areas.

METHODS

The 300-ha oak savanna at CCHNA has been subjected to experimental fires at frequencies ranging from nearly annual burns to complete fire exclusion (Reich et al. 2001). Fires are of low intensity, and burning is conducted in spring before leaf emergence on oaks (see Reich et al. 2001 for details). Unburned areas are dominated by woody plants whereas frequently burned areas contain small patches of oaks and large open spaces dominated by herbaceous plants. Bur oaks occur in all areas, but are a more dominant part of the woody plant community in frequently burned sites (Peterson and Reich 2001).

Corythuca arcuata (hereafter lace bugs) and *Hoplochaitropsus quercicola* (hereafter aphids) are both specialists on bur oak. Lace bug adults and nymphs feed on leaf mesophyll resulting in widespread leaf discoloration and mottling. Aphids feed on phloem through leaf veins; they are tended by thatch ants, *Formica obscuripes*. Both species of herbivores colonize leaves in full sun during late May through early June, and populations build throughout the summer. Both species can be very abundant locally, but rarely co-occur on the same tree.

Herbivore exclusion was initiated in June 2004. It included 30 trees: 10 trees infested with lace bugs (hereafter lace bug trees) in burned areas, 10 lace bug trees in unburned areas, and 10 aphid trees in unburned areas (aphid infestation is very low in burned areas). In June, lace bug trees were identified as those with lace bug adults or egg clutches on at least 20 leaves, and aphid trees as those with ant-tended populations on at least 20 leaves. For each tree, insects were excluded from three branches with 125–175 leaves each; three adjacent branches of similar size served as controls. Our exclusion protocols were designed to limit damage by the focal herbivore only. To exclude lace bugs, adults and egg clutches were manually removed from each leaf on experimental (= exclusion) branches once per week throughout the experimental period (June–October). This approach prevented lace bug nymphs from feeding on exclusion branches because eggs need more than one week of incubation before nymphs emerge; preliminary observations suggested nymphs were much more damaging to leaves than adults. Lace bug adults did recolonize leaves between removal episodes. To exclude aphids from a branch, aphids and ants were removed by hand and then insect sticky trap (Tanglefoot Company, Grand Rapids, Michigan, USA) was placed on sleeves at the base of the branch to prevent ant access. Branches were checked for aphids once per week thereafter. Herbivory levels on unmanipulated (control) branches and exclusion branches were measured in mid-August. For lace bugs, herbivory was estimated from mottling of leaves caused by lace bug feeding. This damage is easy to identify and is always associated with lace bug frass and exoskeletal remains on leaves. Each leaf was categorized as having high damage (mottling on >30% of leaf surface), low damage (mottling visible, but on <30% of leaf surface), or no damage from lace bugs. For statistical analyses, we assigned leaves median values for their damage category (70, 15, or 0) and calculated mean damage per tree on exclusion and control branches. Aphid herbivory level on each control and exclusion branch was estimated from the number of aphids feeding per leaf on five representative leaves. Two trees were dropped from the experiment (one lace bug tree in the unburned area and one aphid tree) because infestation levels on these trees remained low throughout the summer.

Leaf samples from exclusion and control branches were collected for chemical analyses at the onset of the experiment (June), during mid-season (August), and after leaf abscission (October). From each branch, four to five haphazardly selected leaves were collected on each sampling date then dried at 60°C for 48 h. Dried material was ground in a Wiley mill (Thomas Scientific, Swedesboro, New Jersey, USA) through a 40-mesh (0.8-mm) screen; a fraction was then ground to powder in a ball mill (SPEX Certiprep, Metuchen, New Jersey, USA).

For each sampling period, material from each branch was analyzed for total nitrogen (N), phosphorus (P), hemicellulose, cellulose, lignin, cell solubles, and total phenolics. Powdered material was used for measuring elemental concentrations, and ground material was used for measuring C fractions and phenolics. Nitrogen concentration was measured using a Costech Analytical Elemental Combustion System 4010 (Costech Analytical, Valencia, California, USA), and P concentration was determined using persulfate acid digestion and ascorbate–molybdate colorimetry on an Alpkem auto-analyzer (OI Analytical, College Station, Texas, USA). Total phenolic concentration was quantified using the Folin-Ciocalteu micro method (Waterhouse 2002). For standards, tannins were extracted and purified from bur oak foliage using multiple washes of 95% ethanol followed by washes of 70% acetone on a funnel containing Sephadex LH-20 (Sigma-Aldrich 84952, St. Louis, Missouri, USA), and then dry products were obtained using rotary evaporation and lyophilization. Concentrations of hemicellulose, cellulose, lignin, and cell solubles were determined by sequential neutral detergent/acid detergent digestion (Van Soest 1994) on an Ankom 200 fiber analyzer (Ankom Technology, Macedon, New York, USA); the final acid-insoluble fraction was ashed to determine lignin content on an ash-free dry mass basis.

To determine herbivore effects on litterfall chemistry and subsequent decomposition rate, labeled flagging was tied to petioles of haphazardly selected leaves on exclusion and control branches before abscission. In early October, flagged leaves were collected from the forest floor within 24 hours of abscission (trees were checked daily). They were then dried at 60°C for 48 h. For each branch, 5 g of dried leaf material was placed in a 15 × 15 cm litter bag with 0.8-mm polyester mesh. Sides of bags were heat-sealed and the filling end was stapled. In late October, six bags (three exclusion, three control) per tree were fastened to the ground with metal stakes; they were placed in random order at least 0.5 m apart half way between the trunk and drip line of the tree of origin. Each bag contained litter from only one branch, and bags were placed only under the tree of origin.

In addition to our central tests of the environmental condition and herbivore identity hypotheses, we also assessed whether decomposition rate was affected by

lace bug frass and exoskeleton, some of which remain affixed to leaves after senescence. To test this hypothesis, frass and exoskeleton were gently scraped from one 5-g sample of control leaves (pooled from the three control branches) from each lace bug tree ($n = 10$ and 9 trees in burned and unburned areas, respectively). Samples from each tree were then placed in separate litter bags and set out under the tree of origin. Five grams of leaves from lace bug-excluded branches were also scraped to control for effects of scraping damage.

All litter bags were collected in April 2006, 1.5 years after installation. There was only a single collection made because of the limited amount of litterfall available from each branch. After removing non-litter material, bag contents were dried at 60°C for 48 h.

Surveys were also conducted to estimate the effect of fire on levels of herbivory by each insect. In early September, herbivory levels were estimated along three transects in both burned and unburned areas. Along each transect, bur oaks were sampled if they were within 10 m of a transect and were at least 5 m from other sampled trees. Four branches of 125–175 leaves were sampled on each of 10 trees for each transect. Lace bug damage was used as a measure of lace bug herbivory, and leaves were categorized as previously described; mean damage level per tree was used in statistical analyses. Aphid herbivory was estimated from aphid presence/absence. Trees were categorized as having aphids if aphids occurred on at least five leaves on each of the four branches. Trees categorized as having no aphids did not have aphids on any of the surveyed branches. Observations were made from a ladder that allowed access to leaves within ~6 m of the ground.

All statistical analyses were performed using JMP version 5.0 (SAS Institute, Cary, North Carolina, USA). Paired *t* tests were used to compare lace bug damage between exclusion and control leaves; mean values per tree were used in analyses. Nested ANOVAs were used with branch nested within tree to test how herbivory affected decomposition rate and measures of leaf chemistry. Separate analyses were conducted for each herbivore, area, and sampling period. Paired *t* tests were used to test how frass and exoskeleton removal affected decomposition rate. For the herbivory survey, a *t* test (assuming unequal variances) was used to compare mean damage level per tree between burned and unburned areas, and a chi-square test was used to compare aphid presence between areas.

RESULTS

Exclusion treatments significantly reduced herbivory. Weekly removal of lace bug adults and eggs significantly reduced (but did not eliminate) damage in both burned and unburned areas (Table 1). Levels of lace bug damage did not differ significantly between burned and unburned areas on either exclusion (*t* test with unequal variances: $t = 1.631$, $df = 17$, $P = 0.122$) or control branches ($t = 1.402$, $df = 17$, $P = 0.181$). Aphids, which

TABLE 1. Effect of lace bug removal on visible leaf damage.

Fire treatment	Lace bug treatment	Damage level (% of leaves)			<i>t</i>	df	<i>P</i>
		High	Low	No			
Burned	Exclusion	2.1 ± 0.7	86.0 ± 4.0	12.0 ± 4.1	18.716	9	<0.001
	Control	82.6 ± 4.4	15.1 ± 3.3	2.3 ± 1.3			
Unburned	Exclusion	3.2 ± 0.9	63.1 ± 5.7	33.7 ± 6.0	11.843	8	<0.001
	Control	73.9 ± 4.9	24.9 ± 4.6	1.2 ± 0.4			

Notes: Lace bug adults and eggs were removed weekly. High damage is defined as mottling on >30% of a leaf; low damage, mottling visible, but on <30% of leaf. All values are mean ± SE.

did not produce visible damage, were abundant on control branches (240 ± 21 aphids per leaf, mean ± SE; *n* = 135) and were not found on any exclusion branch on aphid trees.

Lace bug and aphid herbivory had different effects on leaf decomposition rate (Fig. 1). Removal of lace bugs led to a significant acceleration of leaf decomposition in both burned ($F_{1,18} = 7.296, P = 0.015$) and unburned areas ($F_{1,16} = 5.263, P = 0.036$), whereas removal of aphids did not significantly affect decomposition rate ($F_{1,16} = 0.422, P = 0.531$). When lace bug data from burned and unburned areas were analyzed together, there were significant main effects of lace bug removal ($F_{1,34} = 16.812, P < 0.001$) and burning (faster decomposition in unburned areas, $F_{1,34} = 66.117, P < 0.001$) on decomposition rate, but no significant removal-by-burn treatment interaction ($F_{1,34} = 0.552, P = 0.462$). Scraping lace bug frass and exoskeletons from leaves did not affect the decomposition rate of control leaves from lace bug trees in burned areas ($t = 0.732, df = 9, P = 0.483$); scraping exclusion leaves also had no significant effect ($t = 0.854, df = 9, P = 0.794$). For trees in unburned areas, removing frass and exoskeletons led to almost significantly slower decomposition ($t = 1.983, df = 8, P = 0.080$), but scraping exclusion leaves (with little affixed frass or exoskeleton

material) produced similar results ($t = 3.048, df = 8, P = 0.015$).

Lace bug and aphid herbivory had different effects on nutrient concentrations in green leaves, but neither type of herbivory significantly altered the nutrient status of senesced leaves (Fig. 2; Appendix). By mid-season (August), lace bug removal had resulted in significantly higher [N] and [P] in exclusion leaves than in control leaves in both burned and unburned areas. However, these differences generally did not carry over to litterfall in October; only P concentration in exclusion leaves from unburned areas remained significantly higher in October relative to controls. Exclusion of aphids had no significant effect on leaf N or P concentration in August or October.

In contrast to its effect on nutrient concentrations, lace bug herbivory had a positive effect on structural investment in green leaves that also existed in litterfall (Fig. 2). In both burned and unburned areas, lace bug removal resulted in significantly lower concentrations of hemicellulose and lignin in green leaf samples in August, and the lower lignin concentration in exclusion leaves was also found in litterfall (Fig. 2; Appendix). Lace bug removal also resulted in a significantly lower concentration of phenolics in litterfall in unburned areas, but had no significant effect in burned areas (Fig. 2; Appendix). Aphid removal did not significantly affect green leaf or litterfall hemicellulose, cellulose, lignin, or phenolics concentrations (Fig. 2; Appendix).

Lace bug and aphid herbivory levels differed between burned and unburned areas. Lace bug damage levels were significantly higher on bur oaks in burned areas than in unburned areas (t test with unequal variances: $t = 7.267, df = 46, P < 0.001$). On trees in burned areas, only 3.3% of leaves showed no lace bug damage and 64.5% had heavy damage (mottling on >30% of leaf surface). In unburned areas, 77.9% of leaves had no lace bug damage and only 6.3% had heavy damage. In contrast, aphids were present on more trees in unburned areas (5 of 24 trees) than in burned areas (1 of 24), a difference that is nearly statistically significant ($\chi^2 = 3.289, P = 0.070$).

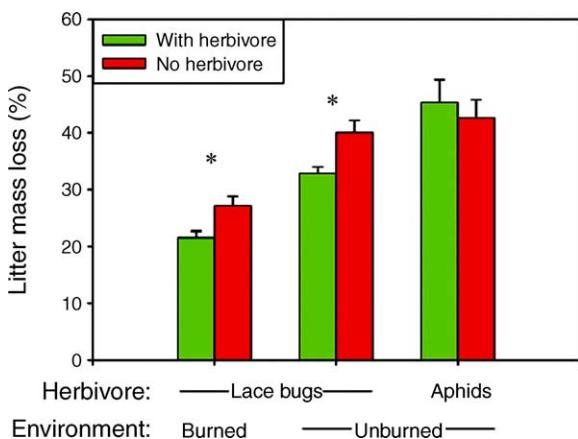


FIG. 1. Effect of herbivore presence and burn treatment on oak litter decomposition rates over 1.5 years. Asterisks indicate a significant effect ($P < 0.05$) of the presence of a particular herbivore within a site. Values are mean + SE.

DISCUSSION

Two main results support the herbivore identity hypothesis, which posits that fire affects the relative impacts of herbivores with different effects on decom-

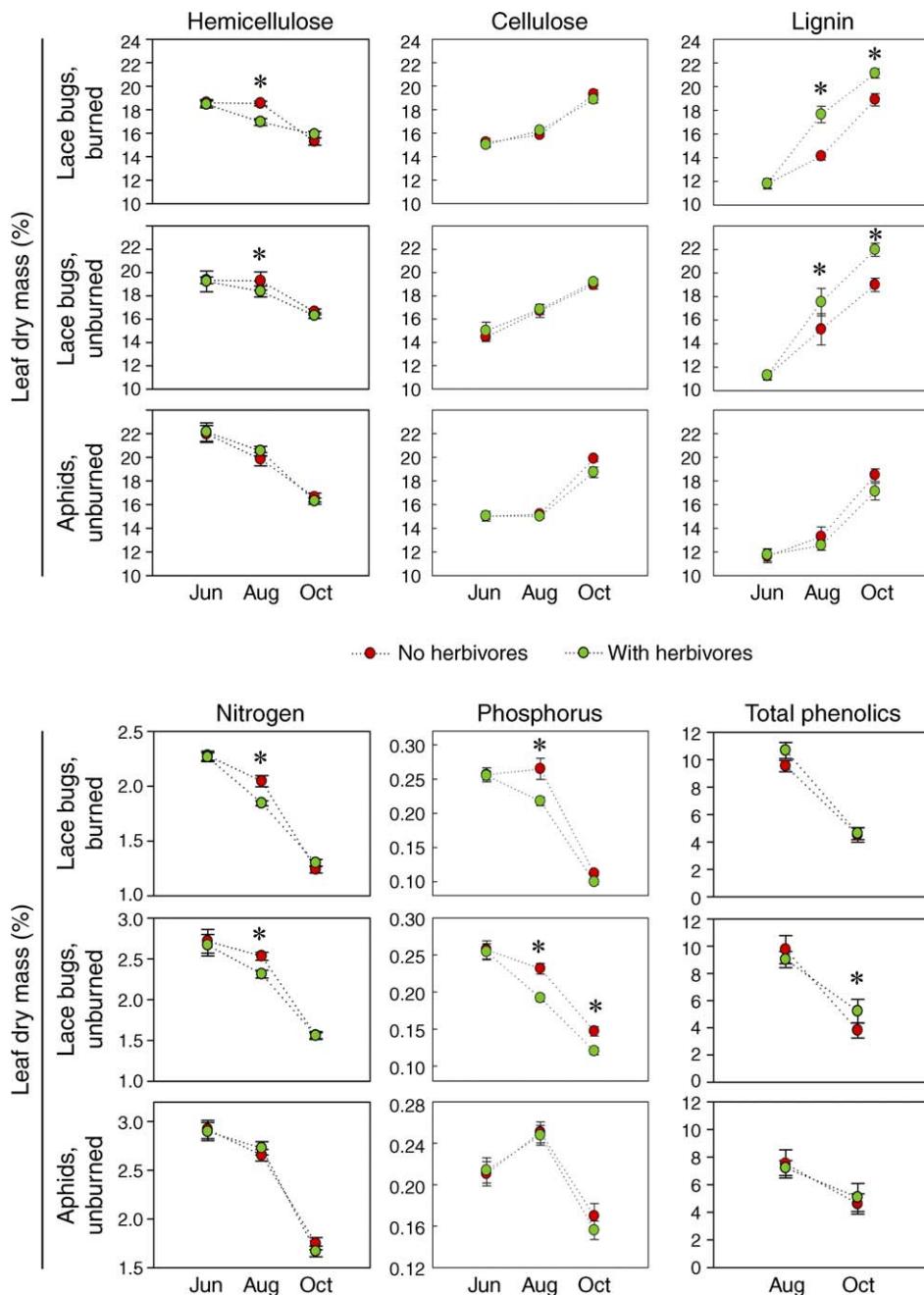


FIG. 2. Effect of herbivory (by lace bug or aphid) and fire (burned or unburned areas) on levels (as percentage of leaf dry mass) of leaf hemicellulose, cellulose, lignin, N, P, and total phenolics. Data are for leaves collected when exclusion began (June), at mid-season (August), and after leaf senescence (October). Asterisks indicate a significant effect ($P < 0.05$) of the presence of a particular herbivore within a site during a sampling period. Values are means \pm SE.

position. First, lace bug herbivory slowed subsequent decomposition by $\sim 25\%$, whereas aphid herbivory had no effect on litterfall chemistry or decomposition rate despite heavy infestation levels. Second, lace bug herbivory was far more common in burned areas than unburned areas, whereas aphid herbivory was not. These results suggest fire promotes oak–herbivore interactions that lead to decelerated rates of litter

decomposition and nitrogen release from litter. We found no support for the environmental conditions hypothesis (fire-related changes in conditions effect herbivore impacts), because lace bug herbivory (where it occurred) had a similar decelerating effect on decomposition in unburned and burned areas.

The effect of lace bug herbivory on decomposition rate was related to lignin. Lignin concentration was

~20% lower in green and senesced leaves from which lace bugs were removed. This result is similar to effects of leaf-galling aphids on cottonwood litter (Schweitzer et al. 2005). It is also consistent with observations by Hall et al. (2005), who found a positive association between lignin concentration and insect herbivore damage in Florida scrub oaks. The negative association we found between lignin concentration and decomposition rate is not surprising, given the well-documented role of lignin in the decomposition process (Melillo et al. 1982). Previous studies on deciduous trees have shown that herbivory can lead to slower decomposition due to induction of bound phenolics that carry over to senesced tissue (Findlay et al. 1996). Lace bug herbivory also resulted in higher concentrations of phenolics in litterfall, but this effect was only found in unburned areas and thus does not provide a general explanation for lace bug-related deceleration of decomposition.

Our leaf and litter chemistry results demonstrate the importance of separating temporary changes induced by herbivore damage from changes that carry over to the litter (Findlay et al. 1996). Lace bug herbivory was associated with lower N and P concentrations in green leaves but not in senesced leaves because nutrient resorption was higher from leaves in the lace bug exclusion treatment. Nutrient differences in green leaves likely affect plant performance (e.g., light use efficiency, canopy C gain) and plant–herbivore interactions (e.g., by affecting foliage quality for herbivores) but they had no direct consequences for litter dynamics.

To our knowledge, our results are the first to demonstrate herbivore-specific effects on the decomposition rate of deciduous leaves due to direct changes in litterfall quality. Such specificity however may be widespread. Different cues of herbivory have often been found to induce distinct plant responses (Hartley and Lawton 1991, Karban and Baldwin 1997), which could differentially affect decomposition if changes carry over to the litter. For example, Schweitzer et al. (2005) argued that gall-forming arthropods may be particularly likely to affect decomposition rates because they can induce changes in lignin and secondary chemical concentrations in galls and surrounding tissue. Similarly, arthropods such as lace bugs that remove leaf mesophyll with piercing mouthparts may consistently lead to slower decomposition if wounding generally increases lignification. Linking specific induced responses to litterfall composition should allow for predictions relating herbivore feeding strategies to nutrient dynamics.

Exclusion of *Hoplochaitropsus quercicola* aphids from particular branches had no effect on bur oak litterfall chemistry or decomposition. This result suggests that aphid feeding does not induce afterlife effects in this system, although we cannot rule out the possibility that aphid honeydew from adjacent leaves contaminated exclusion leaves and masked direct effects of aphid feeding. In addition, aphids may influence decomposition in other ways besides direct effects on

litterfall chemistry. Honeydew can be a major source of carbon inputs under trees (Stadler and Michalzik 1998), affecting leachate composition and microbial activity (Stadler and Müller 1996). *Hoplochaitropsus quercicola* aphids are also obligatorily associated with thatch ants, which have been shown to affect litter decay in other systems (Frouz et al. 1997). Thus, more work is needed before a full comparison can be made between lace bug and aphid effects on litter dynamics.

Our results suggest lace bug herbivory amplifies the decelerating effects of fire on N cycling in this system. Frequent fire leads to a net loss of N due to volatilization; it also reinforces domination by grasses, which is associated with slow root turnover, lower plant nutrient content, and reduced N mineralization rates (Reich et al. 2001, Dijkstra et al. 2006). Fire also leads to increased lace bug density, which is positively associated with the higher light availability and greater concentrations of starch and glucose in bur oak foliage in frequently burned plots (Kay et al. 2007), and lace bug damage, with almost 97% of leaves showing signs of damage in burned plots compared to just 22% of leaves in unburned plots. Because it significantly decelerates decomposition, this increased damage should further depress the N cycle in burned areas. This effect could be significant at the ecosystem level, given that about one-third of the stems in frequently burned plots are bur oaks. More generally, our results show at least in principle how fire-related changes in trophic interactions can impact nutrient cycling.

ACKNOWLEDGMENTS

We thank the University of Minnesota Statistical Consulting Service, Cathleen McFadden for N analyses, Ben Colwell, Michaela Swanson, and Jill Welter for field help, and Maurine Neiman, Seth Wenner, Jessica Monson, and Katie Theisen for helpful comments on the manuscript.

LITERATURE CITED

- Bardgett, R. D., and D. A. Wardle. 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84:2258–2268.
- Boehner, R. E. J. 1982. Fire and nutrient cycling in temperate ecosystems. *BioScience* 32:187–192.
- Chapin, F. S. I., A. J. Bloom, C. B. Field, and R. H. Waring. 1987. Plant responses to multiple environmental factors. *BioScience* 37:49–57.
- Chapman, S. K., S. C. Hart, N. S. Cobb, T. G. Whitham, and G. W. Koch. 2003. Insect herbivory increases litter quality and decomposition: an extension of the acceleration hypothesis. *Ecology* 84:2867–2876.
- Chapman, S. K., J. A. Schweitzer, and T. G. Whitham. 2006. Herbivory differentially alters plant litter dynamics of evergreen and deciduous trees. *Oikos* 114:566–574.
- de Mazancourt, C., and M. Loreau. 2000. Effect of herbivory and plant species replacement on primary production. *American Naturalist* 155:735–754.
- Dijkstra, F. A., K. Wrage, S. E. Hobbie, and P. B. Reich. 2006. Tree patches show greater N losses but maintain higher soil N availability than grassland patches in a frequently burned oak savanna. *Ecosystems* 9:441–452.
- Findlay, S., M. Carreiro, V. Kriskich, and C. G. Jones. 1996. Effects of damage to living plants on leaf litter quality. *Ecological Applications* 6:269–275.

- Frost, C. J., and M. D. Hunter. 2004. Insect canopy herbivory and frass deposition affect soil nutrient dynamics and export in oak mesocosms. *Ecology* 85:3335–3347.
- Frouz, J., H. Santruckova, and J. Kalcik. 1997. The effect of wood ants (*Formica polyctena* Foerst) on the transformation of phosphorous in a spruce plantation. *Pedobiologia* 41:437–447.
- Hall, M. C., P. Stiling, B. A. Hungate, B. G. Drake, and M. D. Hunter. 2005. Effects of elevated CO₂ and herbivore damage on litter quality in a scrub oak ecosystem. *Journal of Chemical Ecology* 31:2343–2356.
- Hart, S. C., T. H. DeLuca, G. S. Newman, M. D. MacKenzie, and S. I. Boyle. 2005. Post-fire vegetation dynamics as drivers of microbial community structure and function in forest soils. *Forest Ecology and Management* 220:166–184.
- Hartley, S. E., and J. H. Lawton. 1987. Effects of different types of damage on the chemistry of birch foliage, and the responses of birch feeding insects. *Oecologia* 74:432–437.
- Hartley, S. E., and J. H. Lawton. 1991. Biochemical aspects and significance of the rapidly induced accumulation of phenolics in birch foliage. Pages 105–132 in D. W. Tallamy and M. J. Raupp, editors. *Phytochemical induction by herbivores*. John Wiley, New York, New York, USA.
- Hunter, M. D. 2001. Insect population dynamics meets ecosystem ecology: effects of herbivory on soil nutrient dynamics. *Agricultural and Forest Entomology* 3:77–84.
- Hunter, M. D., and J. C. Schultz. 1995. Fertilization mitigates chemical induction and herbivore responses of birch feeding insects. *Ecology* 76:1226–1232.
- Karban, R., and I. T. Baldwin. 1997. *Induced responses to herbivory*. University of Chicago Press, Chicago, Illinois, USA.
- Kay, A. D., J. D. Schade, M. Ogdahl, E. O. Wesslerle, and S. E. Hobbie. 2007. Fire effects on insect herbivores in an oak savanna: the role of nutrients and light. *Ecological Entomology* 32:754–761.
- Knight, T. F., and R. D. Holt. 2005. Fire generates spatial gradients in herbivory: an example from a Florida sandhill ecosystem. *Ecology* 86:587–593.
- Kozlowski, T. T., and C. E. Ahlgren. 1974. *Fire and ecosystems*. Academic Press, New York, New York, USA.
- Melillo, J. M., J. D. Aber, and J. F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63:621–626.
- Ojima, D. S., D. S. Schimel, W. J. Parton, and C. E. Owensby. 1994. Long- and short-term effects of fire on nutrient cycling in tallgrass prairie. *Biogeochemistry* 24:67–84.
- Peterson, D. W., and P. B. Reich. 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. *Ecological Applications* 11:914–927.
- Reich, P. B., D. W. Peterson, D. A. Wedin, and K. Wrage. 2001. Fire and vegetation effects on productivity and nitrogen cycling across a forest-grassland continuum. *Ecology* 82:1703–1719.
- Ritchie, M. E., D. Tilman, and J. M. H. Knops. 1998. Herbivore effects and plant and nitrogen dynamics in oak savanna. *Ecology* 79:165–177.
- Schowalter, T. D. 2006. *Insect ecology: an ecosystem approach*. Second edition. Academic Press, San Diego, California, USA.
- Schweitzer, J. A., J. K. Bailey, S. C. Hart, G. M. Wimp, S. K. Chapman, and T. G. Whitham. 2005. The interaction of plant genotype and herbivory decelerate leaf litter decomposition and alter nutrient dynamics. *Oikos* 110:133–145.
- Stadler, B., and B. Michalzik. 1998. Aphid infested Norway spruce are “hot spots” in throughfall carbon chemistry in coniferous forests. *Canadian Journal of Forest Research* 28:1717–1722.
- Stadler, B., and T. Müller. 1996. Aphid honeydew and its effect on the phyllosphere microflora of *Picea abies* (L.) Karst. *Oecologia* 108:771–776.
- Swengel, A. B. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodiversity and Conservation* 10:1141–1169.
- Tilman, D., P. B. Reich, H. Phillips, M. Menton, A. Patel, E. Vos, D. Peterson, and J. Knops. 2000. Fire suppression and ecosystem carbon storage. *Ecology* 81:2680–2685.
- Van Soest, P. J. 1994. *Nutritional ecology of the ruminant*. Second edition. Cornell University Press, Ithaca, New York, USA.
- Wan, S., D. Hui, and Y. Luo. 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. *Ecological Applications* 11:1349–1365.
- Warren, S. D., C. J. Scifres, and P. D. Teel. 1987. Response of grassland arthropods to burning: a review. *Agriculture, Ecosystems and Environment* 19:105–130.
- Waterhouse, A. L. 2002. Determination of total phenolics. Pages 11.1.1–11.1.8 in E. E. Worlsted, editor. *Current protocols in food analytical chemistry*. Wiley, New York, New York, USA.

APPENDIX

Nested ANOVAs for effects of lace bug or aphid exclusion on leaf chemistry (*Ecological Archives* E089-072-A1).