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INSECT HERBIVORY INCREASES LITTER QUALITY AND DECOMPOSITION: AN EXTENSION OF THE ACCELERATION HYPOTHESIS

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Abstract. Herbivore alteration of litter inputs may change litter decomposition rates and influence ecosystem nutrient cycling. In a semiarid woodland at Sunset Crater National Monument, Arizona, long-term insect herbivore removal experiments and the presence of herbivore resistant and susceptible pinyon pines (*Pinus edulis*) have allowed characterization of the population- and community-level effects of herbivory. Here we report how these same two herbivores, the mesophyll-feeding scale insect *Matsucoccus acalyptus* and the stem-boring moth *Dioryctria albovittella* alter litter quality, dynamics, and decomposition in this ecosystem. We measured aboveground litterfall, litter chemical composition, and first-year litter decomposition rates for trees resistant and susceptible to both herbivores and for susceptible trees from which herbivores had been experimentally removed for 16–18 years. Both herbivores significantly increased nitrogen concentration and decreased lignin:nitrogen and carbon:nitrogen ratios of aboveground litter. Herbivory by scale insects also increased litter phosphorus concentration and annual needle litterfall mass. Consistent with its increased chemical quality, litter from herbivore-susceptible trees decomposed more rapidly in the first year. These results suggest that herbivory may increase nutrient cycling rates in this system by altering the chemical quality of litter, a mechanism that augments the nutrient acceleration hypothesis. The distribution of trees resistant and susceptible to the two herbivores at our site, and their associated variation in litter quality and decomposition, likely creates a mosaic of litter quality and nutrient cycling rates at the landscape scale. Further, because the differences in litter quality are associated with tree resistance and susceptibility traits, our findings are among the first to establish that intraspecific genetic variation may affect ecosystem function.

Key words: decomposition; Dioryctria albovittella; *herbivory; lignin; litterfall;* Matsucoccus acalyptus; *nutrient cycling;* Pinus edulis; *pinyon–juniper woodland; Sunset Crater National Monument, Arizona.*

INTRODUCTION

Although insect herbivory is common in terrestrial ecosystems, it has only recently been considered an important and persistent control on ecosystem processes (Schowalter 2000, Hunter 2001) and has not been included as a factor in most ecosystem models. In contrast, several studies of mammalian herbivores have demonstrated important influences of herbivory on nutrient cycling in a variety of ecosystems, ranging from semiarid grasslands to boreal forests (Holland and Detling 1990, Pastor and Naiman 1992, McNaughton et al. 1997, Belovsky and Slade 2001, Helfield and Naiman 2001). Perhaps because of the dynamic nature of some arthropod populations, studies of the influences of insect herbivory on nutrient cycling have often focused on the intense but short-lived herbivory associated with outbreaks (Hollinger 1986, Brown 1994, Lovett and Ruesink 1995). While the effects of severe outbreaks are impressive, the less intense but more persistent insect herbivory present in many systems may also be an important influence on ecosystem processes (de Mazancourt et al. 2001).

In addition to their direct effects on productivity via consumption of plant tissues, herbivores can influence ecosystem function by changing the nature of organic matter inputs to the soil. The chemical composition or ‘‘quality’’ of litterfall and climate are major determinants of decomposition rates and nutrient mineralization (Meentemeyer 1978, Aerts 1997, Kochy and Wilson 1997). Herbivore by-products (i.e., frass, carcasses, honeydew) often have distinctive chemical properties that alter rates of organic matter decomposition and nutrient release within an ecosystem (Hollinger 1986, Lovett and Ruesink 1995, Stadler et al. 2001). Over the longer term, selective herbivory can alter plant community composition, thus altering the dominant litter types available for decomposition (Pastor and Naiman 1992, Ritchie et al. 1998, de Mazancourt and Loreau 2000).

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A less-studied (Irons et al. 1991, Findlay et al. 1996), but often proposed (Choudhury 1988, Grime et al. 1996, Bardgett et al. 1998), pathway by which insect herbivory in particular may impact decomposition and nutrient cycling is through alteration of the chemical properties of litter produced by infested plants. Insect herbivory can change nitrogen (N) and phosphorus (P) concentrations in live foliage and induce production of secondary compounds such as polyphenols and tannins (Schultz and Baldwin 1982, Rosenthal and Berenbaum 1991, Coley and Barone 1996, Karban and Baldwin 1997, Agrawal et al. 1999). If these changes carry over to senescent tissues, litter quality parameters such as carbon:nitrogen (C:N) and lignin:N ratios should also be altered, leading to changes in decomposition rates and subsequent nutrient transformations (Berg and Staaf 1980, Melillo et al. 1982, Scott and Binkley 1997). Herbivore-induced phenolics, carbon-rich compounds that decrease litter quality, have also been implicated as potentially important controls on decomposition (Findlay et al. 1996, Hattenschwiler and Vitousek 2000). Chemical alteration of litter may be especially pronounced when herbivores cause premature abscission of foliage, curtailing nutrient resorption and producing litter with higher nutrient concentrations (Faeth et al. 1981, Williams and Whitham 1986, James and Pritchard 1988, Kahn and Cornell 1989, Karban and Niiho 1995). Despite the abundance of studies on herbivore-induced changes in plant chemical properties, few researchers have investigated the implications of these changes for litter quality, decomposition, and nutrient cycling.

In a pinyon–juniper woodland at Sunset Crater National Monument, Arizona, long-term herbivore removal experiments have demonstrated pronounced effects of insect herbivory at the population and community levels (Brown et al. 2001). Two insect herbivores, with contrasting feeding mechanisms, attack pinyon pines (*Pinus edulis* Pinaceae). A mesophyll-feeding scale insect, *Matsucoccus acalyptus*, infests needles of juvenile trees ($<$50 years), causing needle abscission within a year of infestation. Consequently, scale susceptible trees have sparse, open canopies and lose all but two years of needles, whereas resistant trees have up to eight years of needles. Scale susceptible trees have reduced stem growth, decreased mycorrhizal colonization, and are less responsive to increased moisture than resistant trees (Gehring et al. 1997, Trotter et al. 2002). In contrast to scale insects that attack only juvenile trees, the moth, *Dioryctria albovittella*, attacks and kills terminal shoots and cones of reproductively mature trees ($>$50 years) (Ruel and Whitham 2002). As a result, moth susceptible trees have a shrub-like architecture, reduced female function and mycorrhizal colonization, and altered microbial, bird, and mammal associations (Whitham and Mopper 1985, Gehring and Whitham 1991, Christensen and Whitham 1993, Cobb et al. 2002). When both insects are experimentally removed from susceptible trees (thus far, 16 and 18 years for scale and moth susceptible trees, respectively), tree architecture, growth rates, and mycorrhizal colonization rebound to levels similar to herbivore-resistant trees (Gehring and Whitham 1991, Gehring et al. 1997).

Resistance and susceptibility of pinyon pine to scales and moths appear to be genetically controlled. Mopper et al. (1991*a*) showed that mature trees chronically attacked by moths were genetically differentiated from intermixed trees that suffered low levels of attack. Although similar genetic analyses for scale trees have not been completed, scale susceptible trees are chronically attacked and scale survival is high (i.e., ~70%), whereas intermixed resistant trees support few or no scales and scale survival is low (i.e., ~20%) (Gehring et al. 1997).

We examined how scale and moth herbivory on pinyon pine affects litter quality and dynamics, and how these changes in turn alter litter decomposition rates. We assessed whether two different herbivores, which attack different age classes of trees, would have similar effects on pinyon litter quality and decomposition, thus potentially altering nutrient cycling rates. Ritchie et al. (1998) summarized a positive feedback model, termed the ‘‘nutrient acceleration effect’’, in which herbivory could increase aboveground plant productivity and the rate of nutrient cycling by two mechanisms: (1) selection of nutrient-rich, herbivore-tolerant plants, and (2) production of nutrient-rich, herbivore waste products. In addition to the above pathways, we proposed to test whether herbivores could accelerate nutrient cycling by increasing foliar litter quality. Specifically, we hypothesized the accelerated senescence of foliage caused by scale and moth feeding would reduce nutrient resorption and increase litter N and P concentrations, leading to more rapid litter decomposition and potentially increased nutrient cycling. Because scale insects reduce foliar biomass and tree growth, we also hypothesized that scale susceptible trees would produce less litter than scale resistant and scale defaunated trees. Based on the premature and abrupt defoliation caused by the scale insect, we also predicted that scale herbivory should alter the temporal dynamics of litterfall. We predicted no change in litterfall dynamics due to moth infestation because moth defoliation is less extensive and occurs over a longer period of the growing season than scale defoliation.

METHODS

Site description

This study was conducted at Sunset Crater National Monument (elevation 2000 m) ~30 km northeast of Flagstaff in Coconino County, Arizona (35°22′ N, 111°33′ W). Soils at the site are classified in the soil taxonomic family of cindery, mesic Typic Ustorthents, and consist of lava, ash, and cinders deposited during the eruption of Sunset Crater volcano from ~AD 1064 to AD 1200. Compared to noncindery soils in the surrounding region, cindery soils at Sunset Crater are low in available nutrients and water holding capacity (Gehring and Whitham 1995, Cobb et al. 1997). Dominant plants include pinyon pine, one-seeded juniper (*Juniperus monosperma* Engelm.), Apache plume (*Fallugia paradoxa* D. Don.), Mormon tea (*Ephedra viridis* Coville), and squawbush (*Rhus trilobata* Nutt.). Pinyon pine represents the majority of total woody plant cover, which averages ~40% (Charters 1997). Thirty-year means of annual precipitation and air temperature at a National Weather Service station 10 km west of the study site are 432 mm and 8.6°C, respectively.

Experimental design

Approximately 90% of juvenile pinyon pines at Sunset Crater are infested with the pinyon needle scale, yet very few of these young trees suffer herbivory from the moth. Conversely, moth infestation is common in older, reproductively mature trees, yet these trees are not infested by scale insects. For the past 16 years, scale infestation has been experimentally prevented in a large number of trees by annually removing egg masses found at the base of susceptible trees (Trotter et al. 2002). Moth infestation has been prevented in a group of mature trees for the past 18 years by annual treatments with Cygon, a commercial insecticide (Mopper et al. 1991*a*). We refer to the trees that were initially susceptible but from which the herbivores have been removed as ''defaunated.'' These defaunated trees were established as controls for susceptible trees in order to separate the effects of herbivory per se from differences between resistant and susceptible trees that might be found solely because of tree resistance/susceptibility traits, even in the absence of herbivory. Thus, these long-term removals demonstrated that moths and scales were responsible for changes seen in susceptible trees. Moth and scale defaunated trees have now largely recovered from the impacts of herbivory and resemble resistant trees in canopy architecture and mycorrhizal colonization (e.g., Gehring et al. 1997, Brown et al. 2001). Included in this study were 20 trees from each of these two herbivore removal (defaunated) treatments, plus 20 trees naturally susceptible (and thus infested) and 20 trees naturally resistant to the scale and moth herbivores. Thus, 20 trees in each of 6 different tree categories were used: scale susceptible, scale resistant, scale defaunated, moth susceptible, moth resistant, and moth defaunated, for a total of 120 trees. These 120 trees were chosen at random from their respective groups.

Litter collection and processing

The objective of the litter sampling design was to quantify litterfall from individual trees on a ground area basis. Isoceles triangle litter trap frames were built of 1.9-cm PVC pipe (Reinelt 1991). Each trap sampled 1/20 (18°) of the projected crown area of a tree. One-mm mesh nylon window screening was suspended within the frame. Traps were sized for individual trees so as to extend from the trunk to a distance 20% beyond the drip line, measured from the trunk in the compass direction assigned to that trap. Litter traps were placed under all 20 trees in each treatment, with compass directions being chosen at random without duplication from a set of 20 possible choices (0°, 18°, 36°, . . . , 342°). We collected litter five times over the course of a year from March 2000 to March 2001. Collections occurred in April, June, July, and November of 2000 and March of 2001. These times were chosen to coincide with periods of heaviest litterfall. Litter was sorted into the following four categories: pinyon needles, pinyon wood, pinyon reproductive tissue (cones and strobili), and litter from other species. Litter was oven-dried at 70°C and weighed, after which needle litter was ground to pass through a 40-mesh screen using a Wiley mill (A. Thomas, Philadelphia, Pennsylvania, USA). Needle litter composites were constructed in order to obtain a single sample for chemical analysis representative of the entire year of litterfall from each tree. We created the composite by subsampling a mass of needle litter from each litter collection period proportional to that period's contribution to total annual needle litterfall. Chemical properties were analyzed (see *Methods*: *Chemical analyses*) only for needle litter, which comprised >90% of the total aboveground litter inputs for the juvenile, ''scale'' trees and over 70% of the total aboveground litter inputs for the mature, ''moth'' trees.

Chemical analyses

Lignin analysis was performed on litter composites from 10 trees in each treatment using a modification (D. Turner, personal communication) of the procedure outlined by Iiyama and Wallace (1990). Ten mL of deionized water was added to 15 mg of ground litter and heated at 60°C for 1 h. The mixture was rinsed three times each with deionized water, ethanol, acetone, and diethyl ether. The material was dried overnight at 70°C and then digested with a 25% acetyl bromide solution and perchloric acid for 40 min. The digestate was diluted with 10 mL of 2mol/L NaOH and then brought to 50 mL volume with glacial acetic acid. The samples were refiltered though a large mesh screen and absorbance of the filtrate read on a spectrophotometer at 280 nm (Spectromax Plus 184 Molecular Devices, Sunnyvale, California, USA). National Institute of Standards and Technology (NIST) pine standard (NIST no. 1575) was used as a lignin standard.

All 120 litter composites (20 trees × 6 groups) were analyzed for total N and P using a modified micro-Kjeldahl digestion (Parkinson and Allen 1975) followed by colorimetric analysis on a Lachat flow-injection analyzer (Lachat Instruments 1992*a*, *b*). Total Kjeldahl nitrogen (TKN) and phosphorus (TKP) concentrations were calculated on an ash-free, oven-dry mass basis. Total carbon was quantified using a Carlo-Erba model 2500 CN analyzer (Milan, Italy).

The butanol-HCl method was used to assay tannins (Porter et al. 1986). Condensed tannins were extracted exhaustively with 70% acetone at 4°C. Various tannin extraction methods were tested, and the 24-h extraction recommended by Hagerman and Butler (1989) was used because it produced the highest yield.

Litter decomposition

We designed this experiment to investigate two factors that influence decomposition and which are potentially affected by herbivory: the chemical quality of litter and soil microclimate, the latter being the subject of a separate publication (A. T. Classen, S. C. Hart, T. G. Whitham, and G. W. Koch, *unpublished manuscript*). Therefore, within each herbivore category a partial reciprocal litter transfer was performed that placed two types of needle litter (from herbivore resistant and susceptible trees), under three types of trees (herbivore susceptible, resistant, and defaunated). Source litter was collected over a period of six months from 10 trees in each treatment, mixed, and air-dried. Litter from moth and scale defaunated trees was not included as source litter because preliminary studies showed litter from defaunated trees to be chemically similar to resistant tree litter.

Litter bag design was similar to that used in the LIDET (Long-Term Intersite Decomposition Experiment Team) studies. The bags were 10 × 10 cm, the upper side consisting of 0.8-mm polyester mesh and the lower side (facing the ground) was no. 72191 polypropylene (Synthetic Industries, Atlanta, Georgia, USA). Bags were stitched together with polyester thread and closed at the filling end with stainless steel staples. Decomposition bags placed under trees in the scale experiment initially contained 1.25 g air-dry needle litter, while bags used in the moth experiment initially contained 2.5 g air-dry needle litter. Four pairs of litter bags were fastened to the ground using steel pins at a location midway between the trunk and the tree drip line beneath each of 20 trees in a treatment group. Each pair included one bag containing litter from herbivore-susceptible trees and one containing litter from herbivore-resistant trees. The four pairs were spaced at 90° intervals around the tree, the initial compass bearing being determined by locating one pair +30° from the litter trap. The four pairs were designated for removal 1, 2, 4, and 8 years after installation. This study reports first year decomposition results.

Following air-drying for 1 wk in the laboratory, any nonlitter material in the bag was removed, and the bag contents were dried at 70°C, weighed, and ground. A subsample of the ground litter was combusted at 550°C for 6 h for calculation of ash content and ash-free dry mass.

Statistics

All statistical analyses were performed with the JMP 4 statistical package (SAS Institute 2001). Tests were performed on dependent variables for the three tree classes (resistant, susceptible, defaunation) for each herbivore. One-way analyses of variance (ANOVAs) were used to test for significant differences among treatments for all litter chemistry parameters. Parameters in ratio format (C:N, C:P, lignin:N, lignin:P) were log-transformed prior to ANOVA. Significant ANOVAs were followed by post-hoc Tukey's honestly significant difference (hsd) test to perform multiple comparisons of means. For the decomposition experiment, a two-way ANOVA was performed to test the dependent variables of litter type and tree type with an interaction. Main effects ANOVAs were used to analyze decomposition data after determining that no significant interactions between the variables of litter source and tree type were present. Decomposition data were arcsine transformed in order to account for the nonnormality of proportion mass lost data. One-way ANOVAs were used to test differences between the herbivore classes for the annual total of each fraction of litter fall (pinyon needle, pinyon wood, pinyon other) as well as the cumulative total aboveground litter fall (including all fractions). Repeated-measures analysis of variance was then employed to test whether litterfall mass varied among treatments through time. Significance was defined as $P < 0.05$ unless otherwise noted.

RESULTS

Litter quality

As predicted, both scale and moth herbivory significantly increased litter nitrogen concentration [N] and scale herbivory increased litter phosphorus concentration [P]. Litter [N] of scale susceptible pinyon pines was ~50% higher than for scale resistant and scale defaunated trees (Fig. 1A, $F_{2,58} = 78.3$, $P < 0.001$). The different litter [N] of scale susceptible and scale defaunated trees demonstrates that scales are responsible for increasing litter [N] in susceptible trees. Litter from moth susceptible pinyons had 16% greater [N] than that from moth resistant and moth defaunated trees (Fig. 1B, $F_{2,58} = 8.70$, $P < 0.001$). Moth susceptible litter [N] and moth defaunated litter [N] differed significantly, again implicating the herbivore as responsible for the change in litter [N].

Litter [P] of scale susceptible trees was ~50% higher than both scale resistant and scale defaunated pinyons (Fig. 1C, $F_{2,58} = 10.50$, $P < 0.001$), which did not differ. In contrast to the scale results and counter to our expectation, moth herbivory had no significant effect on litter [P], which was similar among susceptible, resistant, and defaunated trees (Fig. 1D).

As expected from the large changes in [N], litter C:N and lignin:N ratios were decreased by herbivory. The C:N of litter from scale susceptible trees was 38% low-

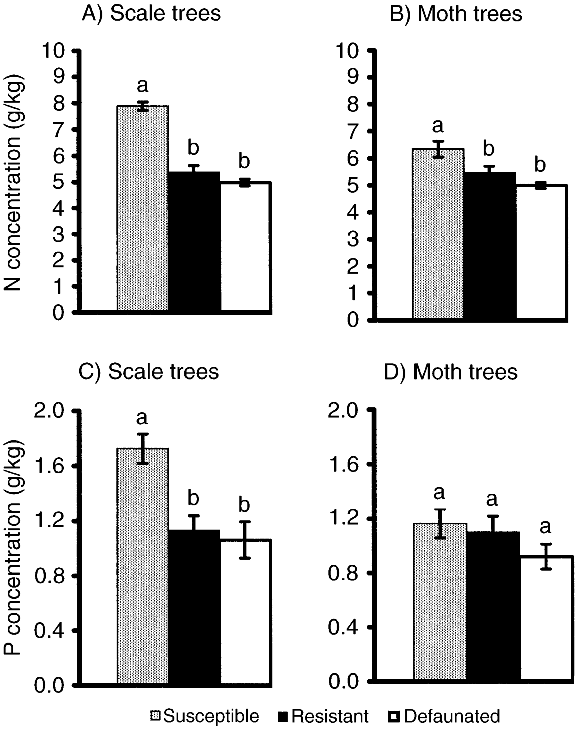

FIG. 1. Influence of insect herbivory on litter N and P concentration at Sunset Crater National Monument, Arizona. $N = 20$ for all litter types. Error bars denote ±1 SE. Lowercase letters indicate significantly different means at the $P < 0.05$ level.

er than that of the scale resistant or scale defaunated trees (Table 1, $F_{2,58} = 73.64$, $P < 0.001$). The C:N of moth-susceptible trees was 34% lower than moth defaunated trees and 17% lower than moth resistant trees (Table 1, $F_{2,58} = 15.81$, $P < 0\ .0001$). The C:N of litter from moth defaunated trees was significantly (12%) higher than resistant trees. Scale herbivory significantly reduced litter lignin:N of susceptible trees relative to scale resistant and scale-defaunated trees (Table 1, $F_{2,28} = 19.78$, $P < 0.001$). Moth herbivory had a similar effect; lignin:N of litter from moth susceptible trees was significantly lower than for moth resistant trees (Table 1, $F_{2,28} = 3.53$, $P < 0.05$). For both herbivores, litter lignin:N was similar for resistant and defaunated trees. Lignin:N and C:N differences were driven mostly by differences in [N] of litter, although differences in lignin concentration did contribute slightly to the divergence of the resistant and susceptible trees.

Litter tannin concentrations were similar across all treatments for both herbivores. However, tannin concentrations were slightly elevated in litter from moth-aged trees as compared to litter from scale-aged trees (data not shown; $F_{1,59} = 3.76$, df = 9, $P = 0.057$).

Litter decomposition

Within the scale-aged trees, a two-way ANOVA showed no significant interaction between litter type (scale susceptible or resistant litter) and location (under scale susceptible, resistant, or defaunated trees), thus a main effects model was used. Both factors, litter type and location, contributed significantly to the model (Fig. 2A, model $P = 0.01$, location $P = 0.028$, and type $P = 0.038$, respectively). Litter from scale susceptible trees decomposed significantly more rapidly than scale resistant tree litter across all locations. Decomposition of both types of litter was faster under scale susceptible and scale resistant trees than under scale-defaunated trees.

Within the moth-aged trees, a two-way ANOVA showed significant differences in decomposition rate attributed to both litter type and location (Fig. 2B, model $P = 0.004$, $P = 0.05$, $P = 0.008$). Again, the interaction between litter type and location was not significant thus allowing a main effects model to be used. Litter from moth-susceptible trees decomposed 14% more rapidly than litter from moth resistant trees ($P = 0.045$). Further, both types of litter decomposed faster under moth resistant trees than under moth defaunated or moth susceptible trees ($P = 0.004$).

Litterfall mass and timing

Despite lower foliar biomass (Mopper et al. 1991*b*), the total annual mass of needle litterfall from scale susceptible trees was significantly greater than that from scale defaunated or scale resistant trees (Fig. 3A, main effects model: $F_{2,58} = 3.78$, $P = 0.029$). When analyzed with repeated-measures ANOVA, needle litterfall mass was significantly different for tree type

TABLE 1. Comparison of nutrient ratios of herbivore susceptible, resistant, and defaunated trees in Sunset Crater National Monument, Arizona.

	Scale			Moth		
Variable	Susceptible	Resistant	Defaunated	Susceptible	Resistant	Defaunated
Carbon	48.41^{a} (0.85)	50.52^{a} (0.53)	50.38^{a} (0.38)	47.46^{a} (1.05)	48.83^{a} (1.11)	51.68^{a} (1.82)
Lignin	18.24^{a} (0.46)	19.11^{a} (0.75)	17.19^{a} (0.28)	19.97^{a} (0.45)	18.99^{a} (0.46)	17.15^{a} (0.45)
C:N	64.24^{a} (1.33)	99.86^{b} (4.64)	106.18^{b} (2.81)	82.30^{a} (3.94)	96.18^{b} (4.09)	110.22^{c} (2.28)
C:P	313.29^{a} (19.50)	575.84^{b} (86.18)	637.09^{b} (79.93)	542.38^{a} (80.68)	581.08^{a} (73.91)	560.25^{a} (80.01)
Lignin:N	23.85^{a} (1.07)	35.51^{b} (3.08)	35.95^{b} (1.48)	23.85^{a} (1.07)	39.51^{b} (3.08)	35.95^{ab} (1.48)
Lignin:P	123.40^{a} (11.56)	200.82^{b} (29.56)	235.51^{b} (38.93)	216.63^{a} (30.44)	294.37^{a} (61.45)	256.57^{a} (43.71)

Notes: Means for each herbivore class are reported with ±1 SE in parentheses. Superscript letters indicate significant differences at the $P < 0.05$ level within a herbivore class.

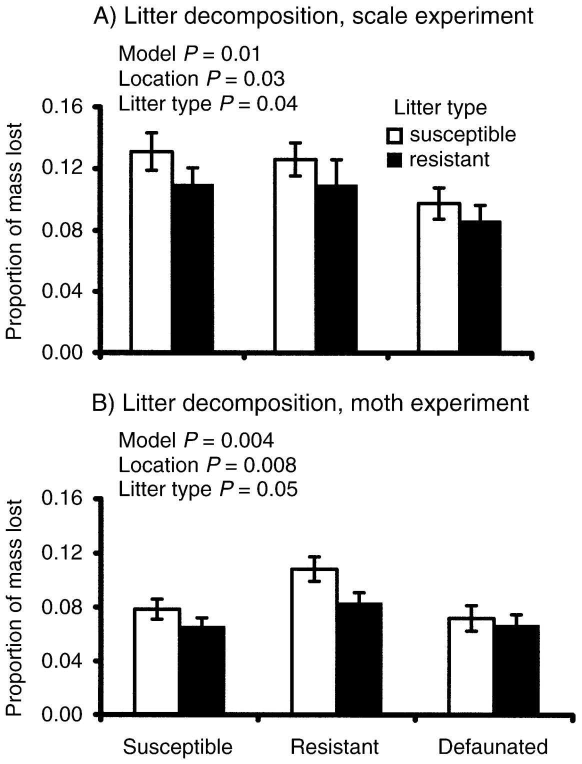

FIG. 2. The effect of herbivore-induced changes in litter quality and site environment on first-year litter decomposition rates at Sunset Crater. $N = 20$ for all treatments. Error bars denote ±1 SE. Statistics (P values) are given for the main-effects two-way ANOVA. Although none of the contrasts between litter types were different within sites, across all three locations there was a significant difference between litter types.

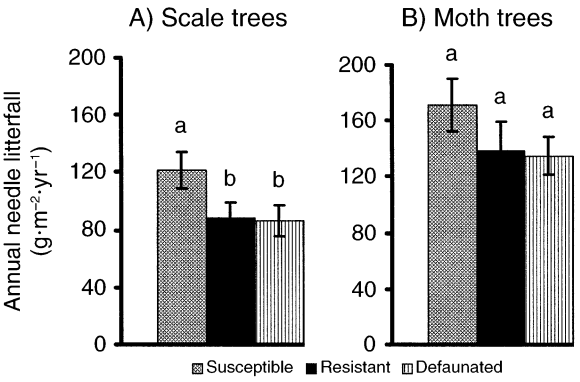

FIG. 3. Annual needle litterfall under juvenile (scale) and mature (moth) trees as influenced by susceptibility to insect herbivory or herbivore removal ($N = 20$, mean ± 1 SE). Lowercase letters indicate significantly different means at the $P < 0.05$ level.

through time (Fig. 4A, $P = 0.040$). The annual "other" litterfall (which includes pinyon reproductive tissue) from scale susceptible trees was one fourth that of scale resistant and scale defaunated trees (main effects model: $F_{2,58} = 6.78$, $P = 0.003$, data not shown). Wood litter mass did not differ significantly among scale defaunated, resistant, and defaunated trees (data not shown). Despite having increased needle litter mass, total litter mass (needles, wood, reproductive tissue) from scale susceptible trees was not significantly different from scale defaunated and scale resistant trees (data not shown).

Moth herbivory did not affect individual fractions of litterfall (needles, wood, other) or total litter production. Annual needle litterfall production was statistically similar for moth susceptible, resistant, and moth defaunated trees (Fig. 3B). When moth needle litterfall mass was examined with repeated-measures ANOVA, there were no significant effects of treatment through time (Fig. 4B).

DISCUSSION

Alteration of foliar chemistry by herbivores is common (Karban and Baldwin 1997), but the implications for litter quality and decomposition are not well understood. Our long-term herbivore-removal experiments demonstrate that two insect herbivores with different feeding mechanisms strongly alter aboveground litter inputs in a semiarid conifer woodland. Herbivory by both scale and moth increases needle litter [N], and decreases the C:N and lignin:N of needle litter (Table 1). In addition, scale herbivory doubles litter [P] and increases the annual needle litterfall (Figs. 1 and 3). The herbivore-induced increase in litter quality translated into accelerated litter decomposition rates. These results confirm our primary hypothesis, that herbivores will increase litter quality and thereby increase litter decomposition rates, and represent one of the first long-

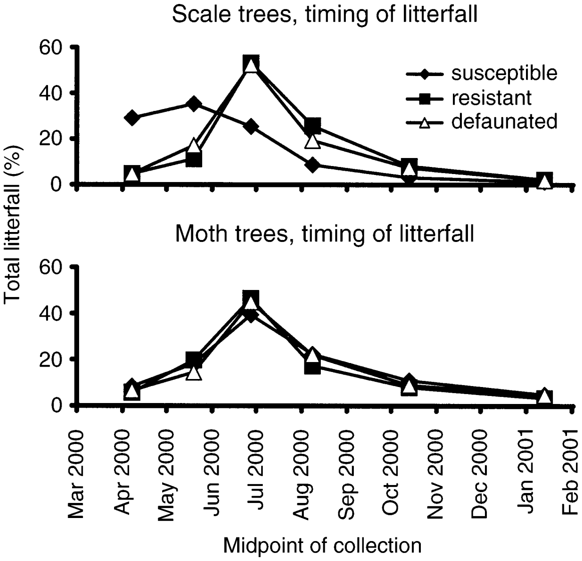

FIG. 4. Timing of annual pinyon litterfall under juvenile (scale) and mature (moth) trees as influenced by susceptibility to insect herbivory or herbivore removal. $N = 20$ for all treatments.

term experimental tests of the role of insect herbivory in regulating nutrient cycling processes. These findings support the nutrient acceleration hypothesis summarized by Ritchie et al. (1998), and add a new mechanism of herbivore influence: the change in litter chemistry of plants subject to herbivory. This mechanism may be as important in many systems as the more widely recognized role of herbivore waste products and herbivore alteration of plant community composition (Hollinger 1986, Holland and Detling 1990, McInnes et al. 1992, Pastor and Naiman 1992, Lovett and Ruesink 1995, McNaughton et al. 1997, Ritchie et al. 1998, de Mazancourt and Loreau 2000, Helfield and Naiman 2001, Stadler et al. 2001).

What mechanisms drive scale and moth alteration of litter chemistry and scale alteration of litter mass?

The probable basis for the observed changes in litter quality is incomplete nutrient resorption prior to early abscission. The *D. albovittella* moth attacks the vascular tissue of terminal shoots, which typically senesce and drop within a few weeks. Hence, because senescing needles typically exhibit gradual declines in [N] and [P] over the year prior to normal abscission (G. W. Koch and N. S. Cobb, *unpublished data*), moth-induced increases in abscission rate should lead to reduced resorption of nutrients. This accelerated senescence likely prevents thorough breakdown of N and P containing compounds, and the loss of phloem function probably inhibits efficient retranslocation from dying needles. The mechanism responsible for increased N and P retention in scale-infested needle litter may be quite different. Although vascular tissue is apparently unaffected (the feeding stylet of scales is in the needle mesophyll tissue), it is possible that scale presence triggers abscission as a defensive mechanism to rid the plant of the herbivore (Karban and Baldwin 1997). It is also possible that the greater amount of litterfall produced by scale susceptible trees stimulates the microbial community, leading to greater nutrient uptake and increased litter quality of scale susceptible trees. If this were the case, one would expect higher [N] and [P] of live tissues of scale susceptible pinyon pines, yet we have found no such pattern for needles or wood (data not shown). Rather, we believe that incomplete nutrient resorption may be an unavoidable consequence of herbivore-induced abscission, a common phenomenon in evergreens (Karban and Baldwin 1997).

Contrary to our predictions, the mass of needle litterfall from scale susceptible trees exceeded that from scale resistant and defaunated trees, despite an obvious reduction in total standing foliar biomass on scale susceptible trees. This implies an increase in foliar turnover due to herbivory, as has been found in other systems (Frank and McNaughton 1993). Because they only have two year cohorts of needles, new foliage production on scale susceptible trees represents a 50% replacement of existing foliage each year, a large increase in proportional allocation of carbon and nutrients to foliage compared resistant and defaunated trees, which replace one out of their five- to eight-year cohorts of needles.

The effects of chronic scale herbivory on aboveground production and turnover in a pinyon pine woodland can be compared to the influence of vertebrate grazing in grasslands (Frank and McNaughton 1993, McNaughton et al. 1997). In those systems, as in ours, herbivory reduces the standing crop of aboveground foliar biomass and increases rates of foliar turnover. However, in contrast to vertebrate grazing, which stimulates total aboveground production by increasing nutrient availability (Frank and McNaughton 1993, McNaughton et al. 1997), tree ring analyses show that scale herbivory (Trotter et al. 2002) and moth herbivory (Ruel and Whitham 2002) decrease annual tree ring increment. This lower annual tree ring production may be indicative of a lower allocation of resources to wood production, thus allowing greater allocation to foliar production. In this system, herbivores reduce the amount of foliar biomass, which cannot be quickly replaced. This reduction in photosynthetic machinery may outweigh any potential positive feedbacks to total aboveground production mediated by enhanced litter quality or subsequent soil nutrient transformations.

Herbivory accelerates decomposition

Needle litter from scale susceptible trees decayed more rapidly than litter from resistant trees during the first year of decomposition, regardless of location (Fig. 2A). This finding supports our prediction that accelerated decomposition will occur due to herbivore-increased litter quality. Both types of scale tree litter (resistant and susceptible) decomposed more rapidly under scale susceptible trees than under scale defaunated trees. Precipitation throughfall, soil moisture, and mean soil temperature are all higher for scale susceptible trees than for scale defaunated and resistant trees (A. Classen, *unpublished data*). These warmer and wetter conditions arise as an indirect consequence of scale herbivory and may be responsible for the higher decomposition rates under scale susceptible trees compared to defaunated trees (Meentemeyer 1978). However, because we have detected no differences in the microclimates of scale defaunated and resistant trees (A. Classen, *unpublished data*), we cannot currently explain why the generally slower decomposition under scale defaunated trees as compared to susceptible trees is not also found under resistant trees. Nevertheless, the ‘‘native’’ comparison reveals that litter from scale susceptible trees decomposes significantly more rapidly under scale susceptible trees than litter from scale resistant trees does under scale resistant trees ($P < 0.05$). Thus, scale herbivory results in more rapid decomposition under natural conditions.

As was true for scale herbivory, litter from moth susceptible trees decomposed more quickly than litter from moth resistant trees. Regardless of litter type, litter decomposition was more rapid under moth resistant trees than under moth susceptible trees. This may be due to slightly elevated moisture levels under moth resistant trees (A. Classen, *unpublished data*). Further, distinct microbial communities are found under trees susceptible and resistant to each of the herbivores (Kuske et al., 2003). Perhaps the microbial community present under resistant trees decomposes litter more quickly than that under susceptible trees. We expected that increased decomposition would also occur under moth defaunated trees due to their architectural, and thus microclimatic similarity, to moth resistant trees. We cannot currently explain why we do not observe this pattern. The native comparison revealed that decomposition of litter from moth resistant trees placed under moth resistant trees did not differ from that of litter from moth susceptible trees placed under moth susceptible trees. Thus, in contrast to the results for scale herbivory, moth herbivory does not appear to alter decomposition during the first year. However, because litter from moth susceptible trees was of higher quality and decomposed more rapidly when analyzed across all locations, higher rates of decomposition under moth susceptible trees may be observed in subsequent years.

How will herbivory affect soil nutrient transformations?

Herbivory by both insects strongly reduced the lignin:N ratio in pinyon pine litter. The resulting range of lignin:N ratio (means ranging from 23–40) found across different herbivore treatments within this single species at one site encompasses much of the range seen across different tree species from diverse forest types (Scott and Binkley 1997). Scott and Binkley (1997) found that lignin:N ratio was strongly and inversely correlated with net N mineralization rates in mineral soil and forest floor horizons. We cannot yet conclude that these herbivores affect soil nutrient transformation rates and thus the full implications of our results await work investigating these processes. Our ongoing studies at Sunset Crater are assessing whether herbivory, which decreased litter lignin:N, has the predicted effect of stimulating N (and perhaps P) mineralization.

Secondary compounds have been implicated as potential controls on decomposition and N transformations (Hattenschwiler and Vitousek 2000). Findlay et al. (1996) found that outbreaking mites increased the amount of N in cottonwood litter. However, due to the plant response to cellular damage, this elevated N was bound in complex phenolic material, rendering it less available for decomposers. We quantified condensed tannins because of their known protein, and thus N, binding capacity. We found no difference in condensed tannin concentration for litter from herbivore-susceptible, resistant, and defaunated trees, and so we assume that there is no increase in tannin-bound N in litter from herbivore-susceptible trees. Thus, the increased [N] in litter from herbivore-susceptible trees likely indicates an increase in N available for release during decomposition and subsequent N transformations.

Genetics and ecosystem processes

Experimental removal of herbivores reversed the insect-induced change in litter quality seen in herbivore-susceptible trees. This demonstrates that herbivory was responsible for the difference in litter properties between susceptible and resistant trees observed in the field. Previous studies in this system have shown genetic differences between moth susceptible and resistant trees (Mopper et al. 1991*a*), and long-term studies suggest that the differences between scale resistant and susceptible trees may also be genetically based (Gehring et al. 1997). Here, we have shown that herbivore susceptibility and resistance influence litter chemistry and decomposition rate via controls on herbivore infestation. The genes responsible for resistance and susceptibility to herbivory in these pinyon pines may indirectly regulate litter quality and thus influence ecosystem processes; however, establishing this link unequivocally will require our ongoing investigations of soil nutrient mineralization rates. Further, given the mosaic of resistant and susceptible phenotypes at the landscape level, herbivory may increase the spatial heterogeneity of important processes in this ecosystem. This mosaic of ecosystem processes is consistent with recent data showing different decomposer and mycorrhizal communities mapping on to herbivore resistant and susceptible trees (Whitham et al. 2003). Soil microbial communities associated with herbivore resistant or susceptible trees may be adapted to process the different qualities of litter inputs at these tree microsites (Hunt et al. 1988, Gehring and Whitham 2002; Kuske et al., 2003). In agreement with Treseder and Vitousek (2001), we found that genetic variation in the plant population at Sunset Crater has the potential to affect ecosystem-level processes.

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