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INSECT CANOPY HERBIVORY AND FRASS DEPOSITION AFFECT SOIL NUTRIENT DYNAMICS AND EXPORT IN OAK MESOCOSMS

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Abstract. Increased nitrogen (N) mobilization and export from terrestrial forest ecosystems following canopy herbivory have been well documented, though the mechanism behind the loss is not clear. Because carbon (C) and N dynamics are closely linked, herbivore activity may also affect C distribution. We initiated a replicated mini-ecosystem experiment to test the hypothesis that insect frass (feces) influences soil C and N dynamics following insect defoliation. One hundred and sixty red oak (*Quercus rubra*) saplings were transplanted to seven-gallon (26.5-L) pots with soil and litter from the Coweeta Hydrologic Laboratory (CWT) (Otto, North Carolina, USA) and overwintered in experimental pot stands. During the 2002 growing season, trees were subjected to a 3×2 factorial experimental design with three damage groups (herbivore, mechanical, ''undamaged'') and two frass depositions (frass, no frass).

Frass deposition increased soil total C, total N, and the soil NH_4^+ pool. Leachate NO_3^- export also increased following frass additions. We suggest that herbivore frass mobilizes sufficient C and N to affect soil pools and N export, though abiotic factors may influence the ultimate fate of the nutrients in frass. In addition, herbivory increased soil respiration and decreased total soil N relative to ''undamaged'' controls independent of frass deposition. While we discuss four possible mechanisms for this observation, we hypothesize that the increased soil respiration results from enhanced root-exudate C and subsequent microbial oxidation. This mechanism has implications for C sequestration and N retention in forest soils. In addition, the effects of mechanical damage consistently did not match those of real herbivory, suggesting that differential responses of *Q. rubra* to damage types also may affect soil nutrient dynamics. Our results demonstrate that the feeding activity of insect herbivores can have direct and indirect effects on the cycling of C and N within the season of defoliation.

Key words: *ammonium; carbon; dissolved organic nitrogen; frass deposition and soil nutrient dynamics; herbivory, real vs. simulated;* Malacosoma americanum; *microbial biomass; nitrate; nitrogen cycling;* Quercus rubra; *red oak; soil respiration.*

INTRODUCTION

In terrestrial ecosystems, aboveground and belowground processes are fundamentally linked by the availability and flow of energy and nutrients (Swift et al. 1979, Wardle 2002). Carbon (C) and nitrogen (N) have received considerable attention, and the dynamics of their distributions are tightly coupled (BassiriRad et al. 2003). Any disturbance that alters the retention and flow of C and/or N in a terrestrial ecosystem can affect the feedback mechanisms between the above- and belowground subsystems. The activity of insect canopy herbivores can alter nutrient dynamics between above- and belowground subsystems (Bardgett et al. 1998, Bardgett and Wardle 2003), and thus may affect the dynamics of the feedbacks between the two (Holland et al. 1996).

The idea that herbivores may affect ecosystem dynamics is not new (Chew 1974), and has received renewed attention (Schowalter et al. 1991). However, the effects of herbivory on ecosystem processes in forests have often been considered inconsequential. Herbivore population densities in forests are often kept low by the activity of natural enemies (Hairston et al. 1960, Slobodkin et al. 1967), the low nutritional quality of the foliage (Haukioja et al. 1985*a*, *b*, Herms and Mattson 1992, Zvereva et al. 1997, Glynn et al. 2003), or both (Hunter and Price 1992). Despite these forces, foliar herbivory has been linked to soil C and N dynamics. The effects of herbivore activity on soil processes have been most pronounced during outbreak events, where N export has been reported (Swank et al. 1981, Reynolds et al. 2000). However, recent evidence also suggests that even endemic levels of herbivory have significant effects on soil processes (Hunter et al. 2003). The loss of N from the terrestrial ecosystem following herbivore activity, largely in the forms of aqueous NO_3^- and dissolved organic nitrogen (DON) (Townsend et al. 2004), disrupts the N cycle and may have aboveground repercussions in N-limited systems. Despite the apparent stimulation of N cycling

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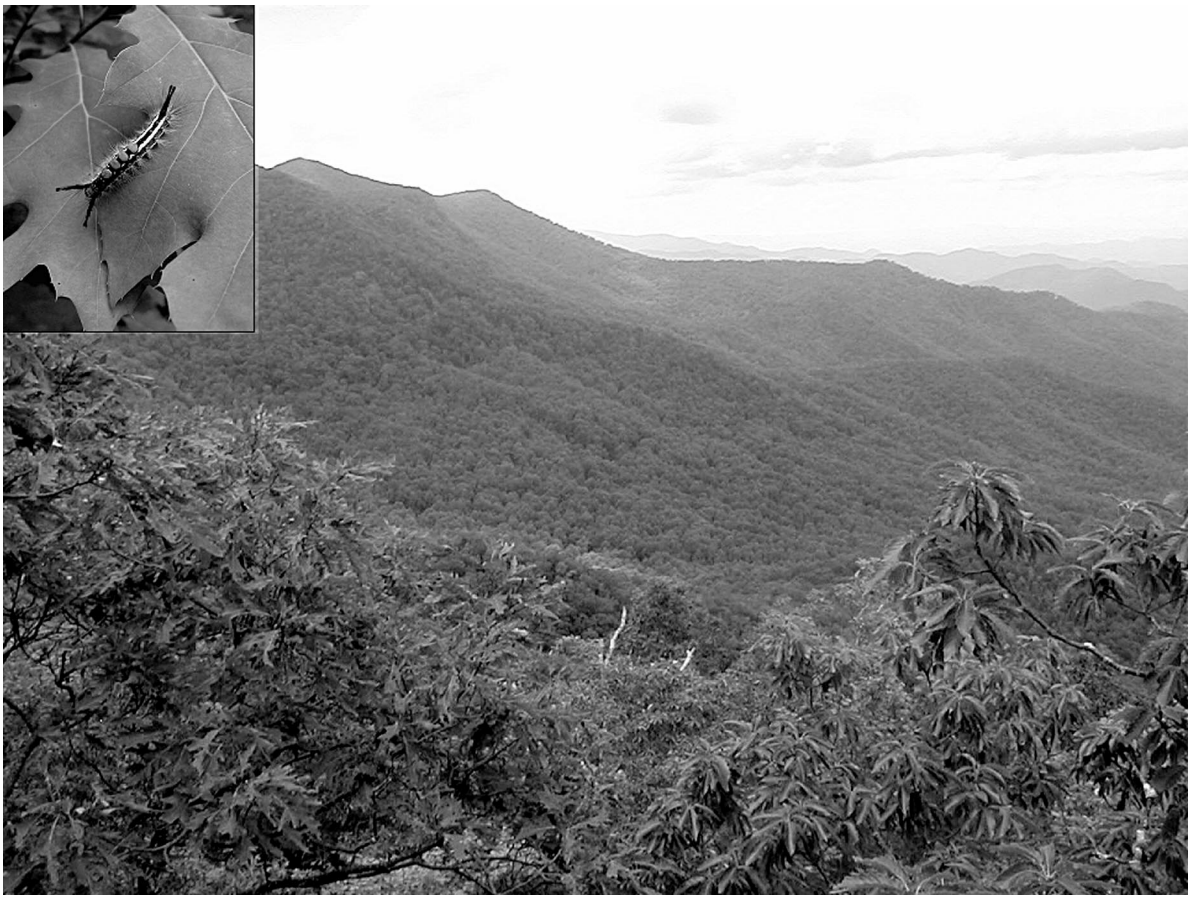

PLATE 1. A photograph of the Coweeta Hydrologic Laboratory in Otto, North Carolina, USA. Observations made in this watershed linking insect herbivores and soil nutrient dynamics inspired the current study. The inset photograph shows a larva of *Orygia leucostigma*, the white-marked tussock moth, a common defoliator of oaks. Photo credit: C. Frost.

and export following herbivory, only recently have efforts been made to evaluate the underlying mechanisms (Bardgett and Wardle 2003), particularly within forests (Ritchie et al. 1998, Lovett et al. 2002). Of the seven possible mechanisms by which insect herbivores can affect soil nutrient dynamics (Hunter 2001), five occur during the season of defoliation (the so-called ''fast cycle,'' sensu McNaughton et al. (1988)): (1) frass (feces) deposition, (2) turnover of insect cadavers, (3) changes in throughfall chemistry, (4) modified plant nutrient uptake rates, and (5) changes in root dynamics including rhizodeposition (exudation) and root–soil microbe interactions. The first three mechanisms are surface soil inputs, while the last two are plant-mediated, belowground responses to herbivory.

The composition of frass has made it an appealing candidate to explain the ecosystem-wide fluxes of C and N following herbivory. Frass is almost entirely organic material and is primarily a labile substrate (Lovett and Ruesink 1995). While frass deposition generally accounts for only 1–4% of annual N deposition in forests (Risley 1986, Risley and Crossley 1988, Hunter et al. 2003), nitrogen returned to soil in frass can exceed that of leaf litter during severe outbreaks (Fogal and Slansky 1984, Grace 1986, Hollinger 1986). Despite this, relatively little is known about the importance of insect frass in nutrient cycling (Bardgett and Wardle 2003), and the few studies explicitly discussing it have offered mixed results. Frass deposition has resulted in increased N mineralization (Lightfoot and Whitford 1990, Reynolds et al. 2000), increased microbial immobilization of N in microcosm and field experiments (Lovett and Ruesink (1995) and Christenson et al. (2002), respectively), and no effect (Reynolds and Hunter 2001).

One interpretation for the inconsistent results is that the effects of canopy herbivory on soil nutrient dynamics may not be entirely explained by increased frass deposition. For example, plants respond to foliar herbivory with a host of species- and condition-specific defenses (Schultz and Baldwin 1982, Rossiter et al. 1988, Hunter and Schultz 1995), and these active defensive responses can extend belowground (Holland 1995, Holland et al. 1996, Ruess et al. 1998). It is known that rhizosphere processes are constrained by the input of photosynthetically derived C (Cheng et al.

1996, Kuzyakov and Cheng 2001), and that these C inputs affect N dynamics (Knops et al. 2002). Thus, the quality and quantity of rhizodeposition in response to herbivore damage may interact with frass deposition to influence the fate of the C and N in the soil system. In this context, one of the proposed mechanisms by which herbivore damage influences N dynamics and plant performance is through insect-specific signals including saliva (Dyer et al. 1995). To account specifically for the differences between herbivores and damage per se, our experiment manipulated both real and simulated (mechanical) damage.

We report here the results of a controlled, factorial experiment to isolate the effects of frass deposition and damage on soil C and N dynamics in a *Quercus rubra* mini-ecosystem. The unique aspect of our study is the ability to explore the effects of frass deposition on soil C and N dynamics independent of aboveground damage and the effects of herbivore damage (real and simulated) on soil C and N dynamics independent of frass deposition. We tested the following hypotheses: (1) frass deposition increases soil mineral N availability; (2) frass deposition increases N export as NO_3^- and DON independent of damage; (3) frass deposition increases soil respiration independent of damage via microbial oxidation of frass C; (4) insect, but not mechanical, damage alters soil C and N pools independent of frass deposition, and (5) herbivore-induced belowground responses by oaks interact with frass deposition to influence soil C and N dynamics.

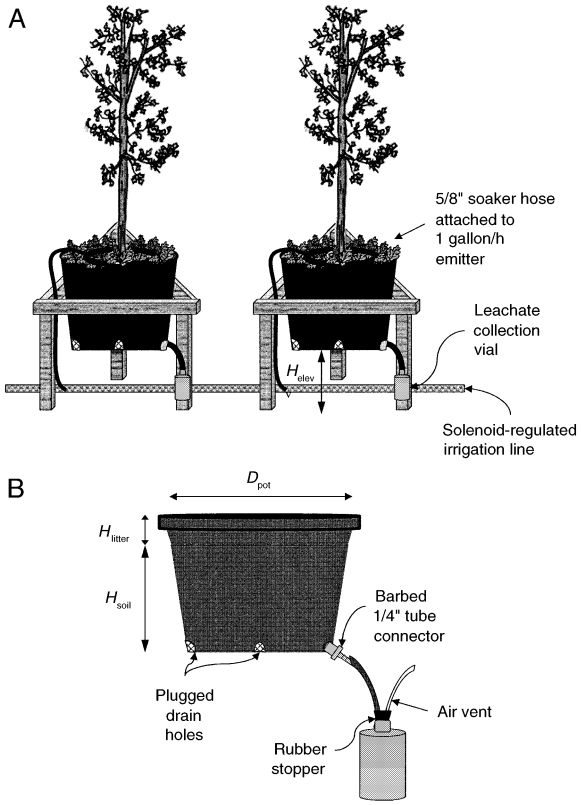

FIG. 1. Design of *Quercus rubra*–soil experimental units. (A) Each sapling was established in a 7-gallon (26.5-L) pot elevated ~25 cm (H_{elev}) above the ground by handmade stands of pressure-treated pine. The experimental array contained 16 rows and 10 columns, totaling 160 experimental units. Two experimental units are shown here, connected by an irrigation line. Each unit was irrigated with a 5/8-inch (1.5-cm) ring-shaped soaker hose that was attached to a 1 gallon-per-hour (3.8-L/h) emitter to ensure uniform watering of the replicates. (B) The diameter of each pot (D_{pot}) was 14 inches (35.6 cm). The depth of the soil (H_{soil}) in each experimental unit was ~24 cm, and the litter depth (H_{litter}) was ~5 cm. See *Methods: Field site* for descriptions of soil and litter collection and preparation. To collect leachate, one of the drain holes was fitted with a tube connector and sealed with silicon caulk. The remaining three drain holes were plugged with caulk. The replicates were used for a 3 × 2 factorial experiment manipulating real and simulated herbivory and frass deposition. Herbivore damage was inflicted by the eastern tent caterpillar, *Malacosoma americanum*, whereas mechanical damage occurred on three days during herbivore feeding. Frass was collected from the herbivore-infested trees (plus an additional 20 trees subjected to herbivore feeding) and distributed among the replicates receiving frass additions. The level of frass deposition was representative of the level of damage experienced by the defoliated saplings. There were 20 individual replicates per treatment for a total of 120 replicates in the experiment.

METHODS

Field site

A field site was prepared in Autumn 2001 adjacent to the University of Georgia Botany greenhouses (Athens, Georgia, USA) using 160 nursery-grown *Quercus rubra* saplings (Forest Keeling Nursery, Elsberry Missouri, USA), transplanted into seven-gallon pots using soil and leaf litter from watershed 27 (''WS27'') at the Coweeta Hydrologic Laboratory (''CWT,'' Otto, North Carolina, USA; elevation 1300 m; see Plate 1). The *Q. rubra* saplings were 1.33 ± 0.14 m tall and averaged 13.71 ± 0.18 (mean ± 1 SE) mm in width (measured 10 cm above the soil surface). Initial height and width measurements did not differ among treatment groups, which are described below. Before collecting soil, the depth of freshly fallen leaf litter at WS27 was first estimated and then we removed and saved all litter from the soil surface area from where soil was collected. The litter was a mixture of different species present in proportion to their representation in the community. At the collection site, the most abundant tree species was *Q. rubra*, though the litter contained leaf material from other taxa. The soil, classified as Typic Haplubrept (Risley 1986), was then collected to a depth of 20–25 cm to match the depth of the experimental pots (Fig. 1). Because of the large volume of soil, soil was roughly mixed and only large roots were removed prior to transplanting. No other additions or deletions were made to the soil. Each experimental pot contained ~21.5 kg of CWT soil. Following transplanting, the surface of the soil was covered to a depth of 5 cm with

the litter removed from above the soil at CWT. The mass of leaf litter in each pot was 45–50 g dry mass equivalent, corresponding to 450–500 g litter/m^2 and approximating the leaf-litter coverage on WS27 at CWT (Risley and Crossley 1988). Once established, the experimental units were allowed to equilibrate for eight months prior to experimental manipulations in 2002. To isolate the experimental units, each was suspended in a triangular stand constructed of pressure-treated pine (Fig. 1). The pots were elevated ~25 cm above the ground to facilitate leachate collection and exclude fire ants, *Solenopsis invicta*, whose presence is ubiquitous in the field. All links to the pots (e.g., legs, irrigation lines) were frequently treated with Tanglefoot® to further prevent fire ant infiltration. We installed an automated irrigation system (Rain Bird, Azusa, California, USA) with a 1-gallon-per-hour (3.785-L/h) emitter and ring-shaped, 1.5-cm soaker hose attached to each pot to ensure consistent and uniform watering. While we irrigated with potentially N-rich tap water, all pots received similar watering regimes. Watering was timed to maintain the soil moisture near field capacity and minimize irrigation-based leaching. As a result, most leaching losses occurred during rainfall events.

Experimental manipulations

We used a 3 × 2 factorial experimental design with three damage (herbivore, mechanical, ''undamaged'') and two frass (frass, no frass) groups. The control group for the damage treatment, ''undamaged,'' is written in quotation marks because the trees experienced low background levels of defoliation (~6% leaf area removed). Twenty experimental units were randomly selected for each of six treatments, totaling 120 experimental units. Because 60 trees required frass additions but only 40 experimental trees received herbivores, 20 additional trees also received herbivores in order to generate sufficient frass to reflect the level of damage.

Herbivore damage was inflicted by the eastern tent caterpillar, *Malacosoma americanum*, in early June 2002. Individuals of *M. americanum* preferentially feed on *Prunus* sp., and we used them as defoliators only because our laboratory supply of white-marked tussock moth, *Orgyia leucostigma*, failed to hatch prior to the experiment. Leaf counts and area measurements were made prior to herbivore additions (1–3 June 2002) with a LI-3000A portable area meter (LI-COR, Lincoln, Nebraska, USA). Total leaf area per tree averaged 9053 ± 3260 cm^3 (mean ± 1 SD), and was not significantly different among treatment groups.

Herbivores were contained within hand-sewn bags of Reemay (Old Hickory, Tennessee, USA) agricultural cloth, and all trees were covered with the bags so that any effects of the bags on trees (e.g., reduced photosynthesis) would occur across all treatments and controls. The bag, a 1.0 × 0.8 m rectangle double sewn on three sides, was placed over the top of each tree and extended downward to cover 65–85% of the total leaf area. Air temperatures inside the bags were approximately 3–5°C higher than outside air temperatures during the day, though no trees showed any signs of heat stress. The bags were secured around the main stem using rope in such a way that herbivores could not escape and frass would collect at the base of the bag without falling through.

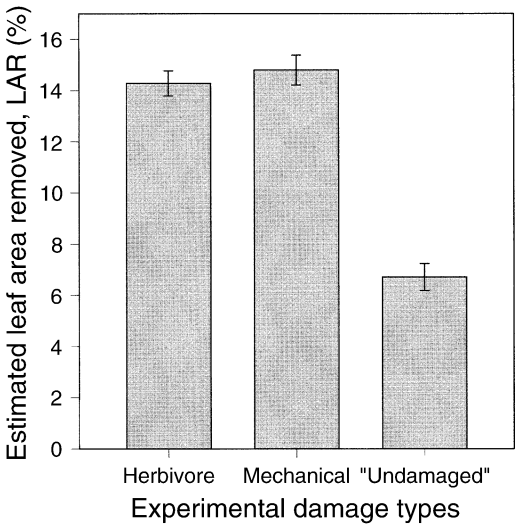

FIG. 2. Estimated leaf area removed (LAR) from *Quercus rubra* saplings in experimental damage groups. Herbivore manipulations roughly doubled background levels of defoliation. Mechanical damage was conducted three times during herbivore feeding. Damage levels generated by the herbivores guided the severity of mechanical damage, resulting in similar LAR between real and simulated herbivory treatments. In addition, the type of damage generated by the herbivores was replicated by the mechanical damage so that similar percentages of individual leaves were removed. Data are the means ± 1 SE of 40 saplings per damage class.

Herbivores were added to trees on 5 June 2002 and removed on 15 June 2002. Thirty 4th-5th instar herbivores were initially added per tree, and visual estimates of mortality were made on a daily basis. The large majority of defoliation by *M. americanum* occurs in the final two instars, and the experimental period of 10 d covers approximately the length of those instars in the field. We estimated damage as leaf area removed (LAR) within two days of the discontinuation of herbivore treatments using techniques described in Hunter (1987). Herbivore activity roughly doubled background levels of defoliation (14.3% LAR vs. 6.7% LAR; Fig. 2). While the damage level was substantially lower than the target value of 40% LAR to replicate outbreak conditions (Reynolds et al. 2000), it was nonetheless significantly higher than ''undamaged'' controls (t_{73} = 10.54; $P < 0.0001$, Fig. 2).

We also simulated herbivory by mechanically removing leaf tissue with scissors. Mechanical damage was imposed simultaneously with herbivore damage and mimicked herbivory in terms of the total leaf area

removed ($t_{75} = -0.69$; $P = 0.4952$, Fig. 2) and the manner in which the foliage was removed. Herbivore damage removed portions of leaf tissue rather than entire leaves; the mechanical damage removed similar amounts of leaf tissue from damaged leaves. Specifically, herbivore-damaged foliage was most often categorized in the 5–30% or 30–50% LAR groups (Hunter 1987), and the mechanical treatment generated foliage within these two damage classes. We also replicated as closely as possible the proportion of leaves damaged, and only leaves that were contained in a bag were clipped by the mechanical treatment. Mechanical damage occurred on three discrete dates (7, 10, and 15 June), while the herbivores fed continuously throughout the 10-d period.

Frass from each herbivore-infested tree was collected by making a small incision in the bag, inserting one end of a modified aspirator (termed ''frasspirator''), and sucking all the frass pellets into the collection vial. The small incision was sealed following frass extraction to prevent herbivore escape. On the same day, the frass collected from each tree (60 total trees) was individually weighed, pooled, and redistributed evenly among the appropriate experimental units. Thus, the amount of frass deposition was representative of the average level of damage experienced by the trees. Frass was collected and distributed twice during the experiment (10 June and 15 June). There were no rainfall events during the period between herbivore additions and the first frass collection from bags. Rainfall (1.5 cm) did occur on the day after the first frass collection, which might have leached some of the nutrients from the frass in the bags. However, only one of five days was influenced by rain and the C and N values in frass were not different between the two collection dates. There was another rainfall event (2.5 cm) on the day following the second frass additions to the soil in pots, following which frass pellets were no longer visible on the soil surface. Overall, the frass additions totaled ~0.982 g frass per tree (dry mass equivalent), corresponding to a deposition of 10 g/m^2, substantially lower than the target ''outbreak'' value of 60 g/m^2 (calculated from Reynolds et al. [2000]).

The frass was composed of 49.13 ± 0.94% C, 3.10 ± 0.05% N (mean ± 1 SE), yielding frass-derived C and N additions of 482 mg (48.2 kg/ha) and 30 mg (3.0 kg/ha), respectively. While this level of frass deposition is roughly 3 times the average annual input of frass at CWT (Hunter et al. 2003), it is only ~17% of that observed under outbreak conditions (Swank et al. 1981, Reynolds et al. 2000). As a result, our experiment tested the hypotheses using herbivore activity and inputs closer to endemic than to outbreak levels of herbivory.

Sampling

Soil N was measured twice (pretreatment and posttreatment) with ion-exchange resin bags and one month posttreatment with a single soil sample. A pair of ion-exchange resin bags, consisting of positively and negatively charged resin contained in lengths of nylon stocking, were used to estimate available inorganic N in the surface soil (Binkley and Matson 1983). On 4 May 2002 the pretreatment set of bags were installed ~3 cm underneath the surface of the soil via insertion holes cut at an angle to minimize the disturbance to the soil above the bags. While placement of the resin bags may have missed nitrification occurring at lower depths and closer to the rhizosphere, we chose the shallow depth because root infiltration can affect the nutrient retention of the ion-exchange matrix and limit the utility of the resin bag technique for understanding rhizosphere processes (Binkley and Matson 1983). Resin bags were removed on 4 June 2002, the day before experimental manipulations, and replaced with a new set of bags that were left for one additional month (until 5 July 2002). The contents of each bag were extracted with 100 mL of 1 mol/L KCl solution and analyzed for NO_3^- or NH_4^+ using the automated cadmium reduction and phenate assays, respectively, on an Alpkem segmented flow autoanalyzer (Alpkem RFA 300; Alpkem Corporation, Clackamas, Oregon, USA). Following extraction, the resin was washed with deionized H_2O, air dried, and weighed.

Bulk surface-soil samples were taken to a depth of 5 cm on 15 July 2002. While the soil sample excluded any short-term soil C and N dynamics, we chose to sample the soil one month following the end of treatments for three reasons. First, the small soil surface area in the pots precluded multiple soil samples. Second, resin bags were installed to estimate N availability during that time. Finally, we were able to collect one month of posttreatment leachate without disturbance to the surface soil that might have affected the results.

Bulk surface soils were passed through a 1 × 1 mm screen mesh to exclude fine roots and separated into three subsamples for separate analyses. The sieving process mixed rhizosphere and bulk soils. Since we did not destructively sample the replicates at the end of the season, the proportion of root biomass collected during soil sampling is unknown. The first subsample of soil was dried for 48 h at 60°C to determine water content, and the dried sample subsequently ground to a fine powder and analyzed for total C and N on a Carlo Erba 1500 C/N analyzer (Milan, Italy). The remaining two samples were analyzed for dissolved organic C (DOC) and bulk surface-soil microbial biomass via the fumigation-extraction method (Vance et al. 1987). Briefly, one subsample was immediately extracted with 50 mL 0.5 mol/L K_2SO_4 on an orbital shaker (150-rpm) and subsequently filtered through Whatman 42 filter paper. We here define this K_2SO_4-extractable soil sample as the soil DOC fraction, which represents a soluble fraction that has been correlated with the labile pool of soil C (Powlson and Jenkinson 1976, Cook and Allan 1992*a*, *b*). The other subsample was subjected to chloroform fumigation for 48 h under reduced pressure,

and then extracted as above. Non-fumigated (S_{nf}) and fumigated (S_f) samples were analyzed with the Shimadzu TOC-500 total carbon autoanalyzer (Columbia, Maryland, USA). Total microbial biomass C was estimated from the difference between S_f and S_{nf}: Microbial biomass C = $(S_f - S_{nf})/k_{ec}$, where k_{ec} is a correction factor based on the efficiency of chloroform fumigation (Sparling and West 1988). Because the mass of soil was low (6–7 g dry mass equivalent), no correction factor (i.e., $k_{ec} = 1$) was used when calculating microbial C (Vance et al. 1987).

Leachate was collected directly from a drainage hole at the bottom of each pot with a collection bottle attached with a length of flexible 1/4 inch (0.64 cm) diameter plastic tubing (Fig. 1). Samples were collected following rainfall events and pooled to correspond with resin-bag data (above). Therefore, leachate collected from 5 May to 4 June 2002 is ''pretreatment'' and leachate collected from 5 June to 5 July 2002 is ''posttreatment.'' Pooled samples were frozen until analysis. Leachates were clear and did not require filtering. Leachate samples were analyzed for total C (TC) on the Shimadzu TOC-500, and for NO_3^- and NH_4^+ as above. Total N (TN) in leachate samples was estimated following persulfate oxidation (Cabrera and Beare 1993), and DON was calculated as the difference between TN and the sum of NO_3^-–N and NH_4^+–N.

Soil respiration was measured weekly from 4 June 2002 to 1 August 2002 with an EGM-2 environmental gas monitor (PP Systems, Haverhill, Massachusetts, USA), which uses a nondispersive infrared measurement technique combined with a soil respiration chamber. We also took three pretreatment measurements over the course of eight weeks (April–May 2002). The first posttreatment measurement was taken after herbivore additions but before frass deposition (10 June 2002), and all remaining posttreatment measurements were subsequent to frass additions. Soil respiration is highly sensitive to soil moisture and temperature. We therefore restricted respiration measurements to between 11:30 and 15:30 hours on rain-free days. Once the chamber was set on the soil, the infrared gas analyzer measured the change in CO_2 concentrations for 60 seconds. Therefore, one replicate could be sampled in ~1.5 min, and the array of 120 soil samples required roughly 3.5 h to sample. We monitored soil temperatures in a random subset of pots during respiration measurements to ensure that soil temperatures were consistent during the sampling period. Soil temperatures and respiration rates were higher than those recorded in the forest from which the soils were collected (see Reynolds and Hunter [2001] for CWT soil respiration rates). Since we were not manipulating soil temperature, all pots experienced the same environmental conditions. Comparing absolute rates of soil respiration between this study and the field is not possible; only comparisons among treatments are meaningful.

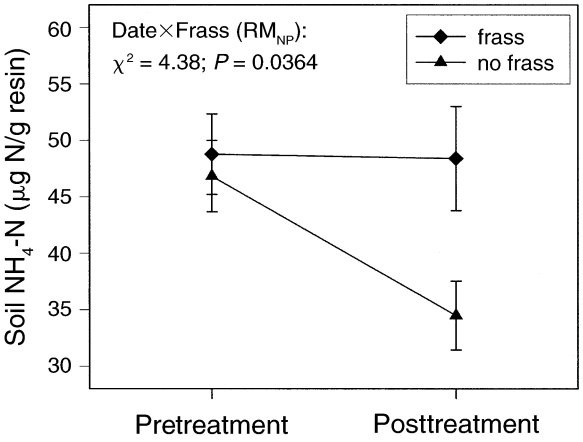

FIG. 3. Soil NH_4-N concentrations in the presence and absence of insect frass as estimated by ion-exchange resin bags. Bags were in the pots for one month (both pre- and posttreatment) and were extracted with 1 mol/L KCl. ''RM_{NP}'' indicates that the data were analyzed as repeated measures with the nonparametric GENMOD procedure (SAS Institute 1998). Points are means ± 1 SE of 60 samples.

Data analyses

Data were analyzed using ANOVA models generated by the GLM procedure of SAS 8.2 (SAS Institute 1998); the residuals of the models were tested for normality (Kery and Hatfield 2003). Parametric repeated-measures models were used when appropriate (signified by ''RM_P''). The data sets whose residuals failed the test of normality were $\log_n$ and/or square-root transformed and reanalyzed. Data that failed these tests were analyzed with the GENMOD procedure of SAS version 8.2, using Poisson distributions and log link functions (SAS Institute 1998). The development of generalized estimating equations (GEE) allows GENMOD to be used as a nonparametric alternative that includes repeated-measures analysis (Littell et al. 2002). The GENMOD procedure reports the χ^2 statistic, and we use ''RM_{NP}'' to denote nonparametric repeated-measures analyses. Posthoc analyses of treatment means are not performed with GENMOD. We used the Student-Neuman-Keuls (SNK) post hoc test ($\alpha = 0.05$) to distinguish among treatment means following parametric analyses. In all cases, the outcomes of the statistical analyses were identical regardless of whether parametric or nonparametric tests were used on the nontransformed data.

RESULTS

Soil mineral nitrogen pools

Despite the small addition of frass, significant effects on soil and leachate N pools were detected independent of damage. The concentration of NH_4–N in soil was higher relative to frass-free controls following frass deposition (RM_{NP} $\chi^2 = 4.38$, $P = 0.0364$, Fig. 3). Total soil N was also higher in pots with frass deposition

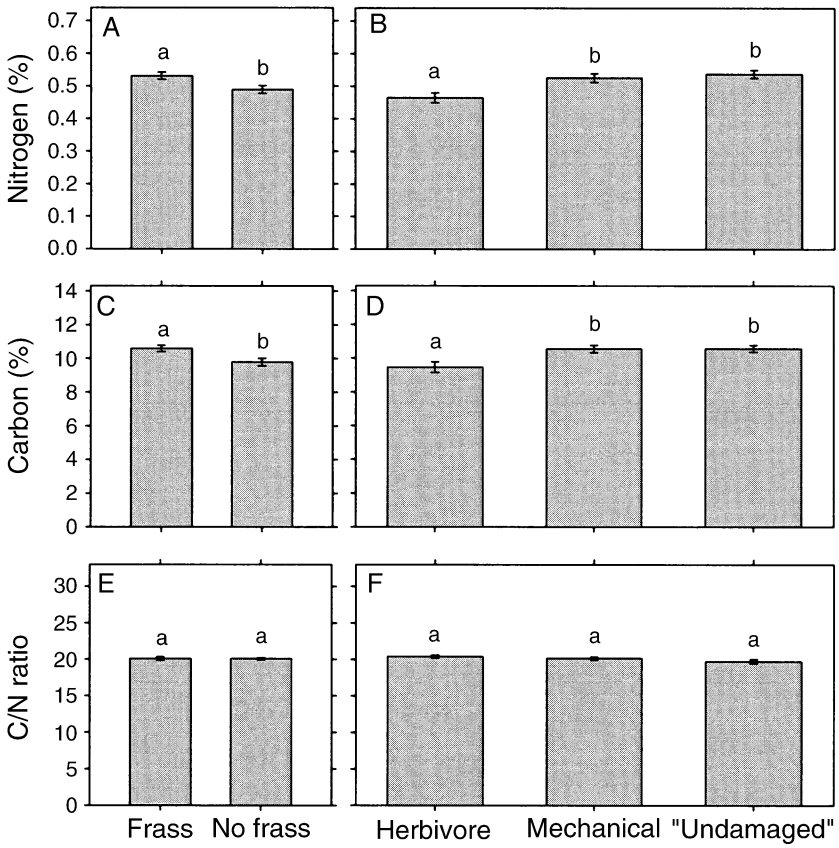

FIG. 4. Total C and N concentrations from soil extracts under frass and defoliation treatments on *Quercus rubra*. Within a panel, bars with different lowercase letters indicate statistically significant differences between treatment groups using the SNK post hoc test ($\alpha = 0.05$). Data are the means ± 1 SE of 60 samples (frass treatments) and 40 samples (damage treatments).

($F_{1, 104} = 7.76$, $P = 0.0064$, Fig. 4A). Based on previous results (Reynolds et al. 2000, Hunter et al. 2003), we expected elevated soil NO_3−N concentrations following frass deposition. Contrary to this expectation, frass deposition did not increase soil NO_3−N concentrations (RM_{NP} $\chi^2 = 1.08$, $P = 0.2983$, data not shown).

In addition to frass effects, herbivory affected soil N pools independent of frass deposition. There was a date × damage effect on soil NO_3^- (RM_{NP} $\chi^2 = 7.01$, $P = 0.0301$, Fig. 5A). Total soil N was also lower in herbivore-damaged systems ($F_{2, 104} = 8.35$, $P = 0.0004$, Fig. 4B). There were no significant damage × frass interactions with soil N in any form. As expected, between-date soil NO_3^- and NH_4^- measurements were positively correlated ($r = 0.432$, $P < 0.001$ for NO_3^-; $r = 0.418$, $P < 0.001$ for NH_4^+).

Nitrogen leaching as nitrate and DON

Leachate NO_3^- concentrations positively correlated with soil NO_3^- concentrations on both dates ($r = 0.272$, $P = 0.0035$ for pretreatment; $r = 0.492$, $P < 0.001$ for posttreatment), and the leachate measurements were themselves positively correlated ($r = 0.250$, $P = 0.007$). Nitrate concentrations in leachate increased across treatments between May and June 2002, but concentrations were significantly greater following frass deposition relative to frass-free controls (RM_P $F_{1, 107} = 6.47$, $P = 0.0124$, Fig. 5B). There were no treatment effects on leachate NH_4-N, and concentrations were low. Low NH_4-N concentrations in leachate is parsimonious with NH_4^+ adsorption to negatively charged soil particles (Quemada et al. 1997), which effectively abiotically immobilizes the NH_4-N and prevents its loss via leaching. While the total concentration of DON-N increased between pre- and posttreatment samples (from 1.20 ± 0.13 to 3.03 ± 0.26 mg/L, $P < 0.0001$), percentage of DON-N in leachate was consistent (24.0% and 27.5%, respectively, $P = 0.2328$). Neither the total amount nor percentage of DON-N were affected by frass deposition ($P = 0.8776$ and $P = 0.5576$, respectively) or damage ($P = 0.8092$ and $P = 0.4553$, respectively). Some DON values were slightly negative (because DON is calculated as a difference between TN (total N) and [NO_3-N + NH_4-N]) and thus treated as 0 for purposes of calculations. There were no significant damage × frass interactions with leachate N in any form.

Soil respiration, DOC, and total carbon

Surface soil microbial biomass C was higher in frass-treated systems ($F_{1, 102} = 5.70$, $P = 0.0191$, Fig. 6).

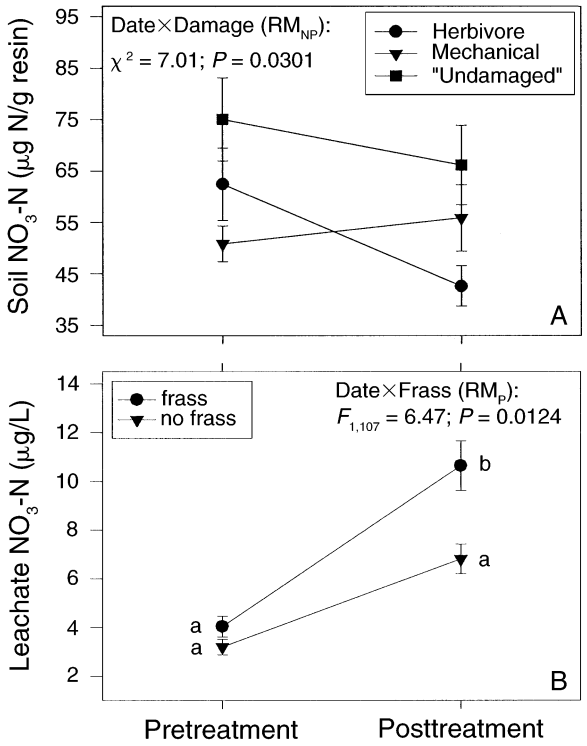

FIG. 5. Concentrations of NO_3-N in soil extracts and leachate from *Quercus rubra* mini-ecosystems. (A) Soil NO_3-N concentrations under three defoliation treatments were estimated by ion-exchange resin bags extracted with 1 mol/L KCl. ''RM_{NP}'' indicates that the data were analyzed as repeated measures with the nonparametric GENMOD procedure (SAS Institute 1998). Points are the means ± 1 SE of 40 samples. (B) Leachate NO_3-N compared between frass treatment groups. ''RM_P'' indicates that data were analyzed as repeated measures using the parametric ANOVA. Different letters within each date indicate statistically significant differences between treatment groups using the SNK post hoc test ($\alpha = 0.05$). Data points are the mean ± 1 SE of 60 samples.

However, frass deposition did not increase soil respiration over the course of the experiment using our method of weekly measurements (RM_P $F_{10, 1050} = 0.54$, $P = 0.8003$, data not shown). Since we did not measure soil respiration in the hours following frass additions, it is possible that we missed a finer resolution of soil respiration responses to frass additions. This seems likely considering the apparent frass-derived increase in microbial C.

Soil respiration increased following herbivore damage relative to ''undamaged'' controls independent of frass deposition (RM_P $F_{20, 1050} = 2.07$, $P = 0.0118$, Fig. 7). The herbivore-mediated increase in respiration was significant within 10 days of herbivory and was maintained throughout the duration of respiration measurements (almost two months). While the effect was pronounced following herbivory, mechanically damaged systems also responded with increased soil respiration on two posttreatment measurement dates (Fig. 7). However, the date × damage interaction was not significant when just mechanically damaged and ''undamaged'' control systems were considered (data not shown).

Soil DOC was higher in herbivore- and mechanical-damage treatments relative to ''undamaged'' controls in the absence of frass deposition (damage × frass $F_{2, 103} = 3.78$, $P = 0.0260$, Fig. 8: no frass). The effect disappeared in frass-addition treatments (Fig. 8: frass). Conversely, total soil C was lower in herbivore-, but not mechanically damaged, pots relative to ''undamaged'' controls independent of frass deposition ($F_{2, 104} = 6.87$, $P = 0.0016$, Fig. 4D). Total soil C was higher in frass-treated pots relative to frass-free pots ($F_{1, 104} = 7.56$, $P = 0.0071$, Fig. 4E). When total soil C and N data were taken together, the higher concentrations following frass deposition and lower concentrations following herbivory resulted in C:N ratios that were not significantly different from either frass-free or ''undamaged'' controls ($F_{2, 104} = 0.020$, $P = 0.888$, Fig. 4E and $F_{2, 104} = 1.11$, $P = 0.3337$, Fig. 4F, respectively). In addition, there was a strong positive correlation between soil total C and N values ($r = 0.90$, $P < 0.0001$).

These results suggest that foliar herbivory stimulated some form of belowground biological activity independent of surface inputs (i.e., frass deposition). Leachate samples were tested for total C and, while there was a decline in leachate C over time ($P = 0.0274$), the decline was not mediated by damage ($P = 0.3372$), frass ($P = 0.7543$), or the interaction of the two ($P = 0.0904$). Therefore, the stimulation of belowground C fluxes following herbivory did not increase C export in leachate.

DISCUSSION

This experiment was designed to test the hypotheses that frass deposition from canopy herbivory increases

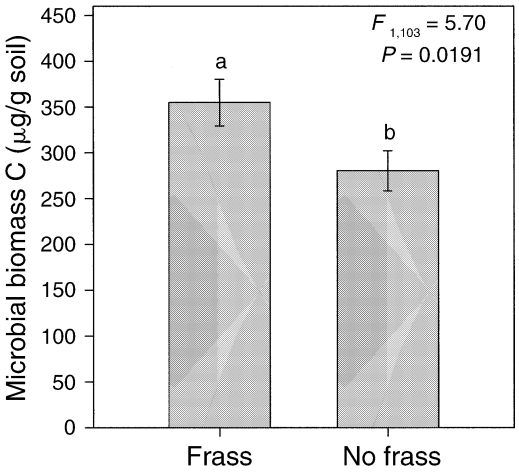

FIG. 6. Soil microbial biomass C, as estimated using the fumigation–extraction method, compared between frass-treatment groups. Different letters above the bars indicate statistically significant differences between treatment groups using the SNK post hoc test ($\alpha = 0.05$). Data are the means ± 1 SE of 60 samples.

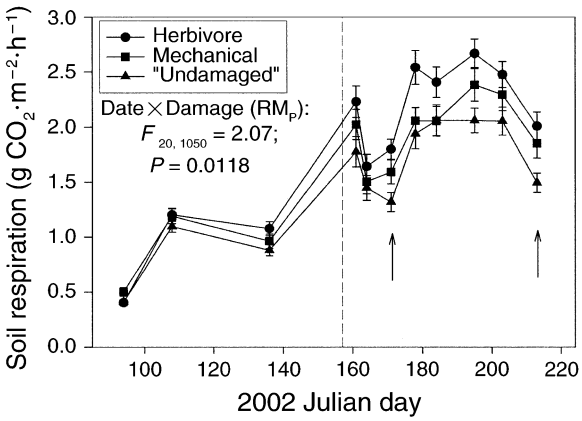

FIG. 7. The response of soil respiration to defoliation treatments on *Quercus rubra*. Soil respiration measurements were made in situ with a portable soil-respiration meter. "RM_P" indicates that data were analyzed as repeated measures using the parametric ANOVA. The herbivore damage group was statistically different ($\alpha = 0.05$) from the control group for each of the last six sampling dates presented. The dashed vertical reference line represents the initiation of experimental manipulations (5 June 2003, Julian day 156 [1 January = Julian day 1]). The mechanical damage group was statistically different ($\alpha = 0.05$) from the control group on the dates indicated; the arrows indicate where the mechanical treatment differed from undamaged. Data points are means ± 1 SE of 40 samples.

soil N, aqueous N exports, and soil respiration. While we were unable to replicate the level of damage (and thus frass deposition) of outbreak conditions, the data tell three equally interesting stories about canopy herbivory and nutrient dynamics at closer-to-endemic levels. First, frass deposition increases soil N pools and accelerates N export from the terrestrial system. Second, mechanical damage did not generate the same belowground responses as did real herbivory. Third, aboveground herbivory on *Quercus rubra* affects soil C and N pools independent of frass (or other surface) additions.

Frass deposition

Our results provide evidence that frass deposition from herbivore activity can account for increases in the soil inorganic N pool and the N lost from the terrestrial system via leaching during the season in which the defoliation occurs. Since the differences in soil mineral N and leachate NO_3^- were observed between pots receiving frass and those that did not, we can say that frass deposition has an effect on soil N dynamics. While we assume that the N in the frass is the N observed in leachate NO_3^- and soil NH_4^+, we are currently conducting a stable-isotope ^{15}N-labeled frass experiment to confirm this hypothesis.

Contrary to increased soil NO_3^- levels found in the field under endemic (Hunter et al. 2003) and outbreak (Reynolds et al. 2000) conditions, our data indicate relative increases in NH_4^+, but not NO_3^-, in response to frass deposition. The difference in form may be an artifact of the oak mesocosm, because *Q.rubra* tend to inhibit nitrification (Verchot et al. 2001). Another possibility is that the resin bags buried at 3 cm did not detect increased NO_3^- because nitrification may have occurred at lower soil depths, especially considering increased leachate NO_3^- implies increased soil NO_3^- concentrations. While the form of inorganic N is different, the overall message is the same: insect herbivores influence soil inorganic N availability via frass deposition. From our perspective, the interesting result is that the systems responded to relatively small frass additions. Forest soil N pools are dependent on annual surface inputs of leaf litter (Risley 1986, Risley and Crossley 1988, Hunter et al. 2003), and it is increasingly clear that insect herbivore activity influences litter quality and subsequent decomposition (Chapman et al. 2003). Nitrogen mobilized in frass is the same N that would enter the soil as leaf litter in the absence of herbivores. Herbivore activity consequently can change the timing and/or form of N deposition but may not affect the total amount of N inputs to the soil. However, the measurable increase in soil N following even modest frass deposition apparently has consequences for how the total N is ultimately distributed.

Considering N loss from the terrestrial system, our data are consistent with results from previous field observations at Coweeta National Laboratory CWT (Swank et al. 1981). Reynolds et al. (2000) linked frass deposition from an outbreak event at CWT with elevated NO_3^- levels in the stream that drained the defoliated watershed. Nitrogen lost as leachate NO_3^- cannot be recycled through the terrestrial system in which it had been immobilized as leaf tissue. As far as we

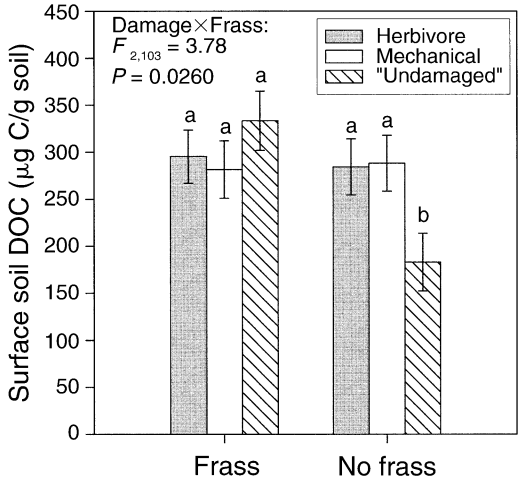

FIG. 8. Surface soil DOC (dissolved organic carbon) measurements in *Quercus rubra* mini-ecosystems. Soil samples were taken one month following damage treatments and frass additions. DOC is here defined as the K_2SO_4-extractable fraction of soil C. Bars with the same lowercase letters above indicate statistical similarity via the SNK post hoc test ($\alpha = 0.05$). Data are means ± 1 SE of 20 samples.

know, our data are the first to demonstrate that frass deposition represents a mechanism by which herbivore activity can increase stream nitrate concentrations. Even at relatively low levels, insect herbivore activity may therefore simultaneously influence N dynamics in a forest and its associated aquatic ecosystem. However, ''loss'' from a pot may not equal ''loss'' from a forest ecosystem if other conservation mechanisms operate.

Stadler et al. (2001) report that excreta from aphid and lepidopteran larval feeding did not change the size of mineral N pools in the soil. They suggested that the effects of aboveground herbivory were obscured in the soil by ''buffering biological processes'' (Stadler et al. 2001:104). A similar conclusion was reached by Lovett and Ruesink (1995), who found net N immobilization of substantial amounts of frass N relative to soil following incubation in closed microcosms. In contrast, Hunter et al. (2003) found increased soil NO_3^- concentrations following endemic levels of frass deposition in the field, and the data reported here support those results. Our fifth hypothesis, interaction between frass deposition and belowground responses to damage affecting soil C and N dynamics, was conceived to explain the variation in reported results of frass deposition on soil N. The data do not support the hypothesis: frass deposition and herbivory influenced soil C and N dynamics independently.

Instead of the interaction between frass deposition and belowground responses to aboveground herbivory, variable results among published studies might be reconciled by considering the interaction of precipitation and frass deposition. For example, Lovett and Ruesink (1995) maintained high moisture contents inside their microcosms, did not flush them with solution, and visible fungal hyphae infiltrated the frass pellets. We have observed similar phenomena in recently conducted microcosm and field studies (C. Frost, *personal observation*). Conditions of high humidity and low rainfall apparently allow rapid immobilization of frass N by soil fungi, and we would correspondingly predict minimal leaching losses of N. In the absence of rainfall, frass pellets deposited on the soil surface of a hybrid poplar stand in Michigan (USA) remained visible and undecomposed, and no increases in soil mineral N were observed (referenced as a ''personal communication'' in Hunter [2001:78]). During our experimental manipulations, rainfall events occurred within two days of frass additions, and the frass pellets were not visible the day after the rainfall. Historical precipitation data at CWT show rainfall events during the peak periods of herbivore activity in the studies that have correlated defoliation and N export (Swank et al. 1981, Reynolds et al. 2000). Assessing our data in the context of the other published studies, herbivore activity evidently mobilizes sufficient N as frass to affect soil N pools and export even at endemic herbivore densities, though the ultimate fate may depend on the relative timing of frass deposition and precipitation.

Our third hypothesis, that frass deposition would increase soil respiration, was not supported using our sampling regime despite an apparent stimulation of the surface soil microbial community. Similarly, a field study at CWT by Reynolds and Hunter (2001) found no relationship between soil respiration and frass deposition at double background levels. Soil microorganisms are thought to be C limited (Cheng et al. 1996), and our experimental frass deposition may not have supplied enough labile C to elicit a noticeable difference. Our experimental additions supplied ~482 mg C to the soil in the form of frass, some of which was in the form of recalcitrant phenolics (Kopper et al. 2000). The additional respiration measured following herbivory alone roughly amounted to 100 mg C/h, which would exceed the total amount of C added as frass within five hours. Therefore, it is not surprising that the direct contribution of frass C to soil respiration was not detected with our sampling regime. In our system, the contribution of roots to total soil respiration possibly masked any frass effect. Lovett and Ruesink (1995) found a positive effect of frass on respiration using large quantities of frass relative to soil in a root-free controlled environment, though the effect was shortlived. These results collectively suggest that (1) a threshold level of frass deposition may be required to elicit a response in soil respiration above background levels, (2) the response will be ephemeral, and (3) the C added as frass remains in the surface-soil horizons.

Real vs. simulated herbivory

To our knowledge, this is the first reported study to test the responses of belowground nutrient fluxes to real and simulated herbivory. In our experiment, mechanical damage failed to generate soil C and N fluxes comparable to real herbivore activity. Mechanical damage can elicit a number of tangible responses, including increased photosynthetic rate in oaks (Lovett and Tobiessen 1993) and reduction in seed pod production in vetch (Koptur et al. 1996). However, differential effects of real and simulated herbivory have long been recognized (Baldwin 1988*a*, *b*). The focus of the studies testing for differences between real and simulated herbivory have been limited to aboveground direct (Litvak and Monson 1998) or indirect (Alborn et al. 1997, Kainoh et al. 1999, Hoballah and Turlings 2001, Oppenheim and Gould 2002) defensive responses. The mechanisms underlying the differences have been identified in some cases (Bergman 2002). We are unable to provide a specific mechanism for our observation, though we hypothesize that there is a signaling pathway by which oaks recognize the presence of insect herbivores and engage herbivore-specific defensive responses (Dyer et al. 1993, 1995) that extend belowground. This result suggests that the response of oaks to disturbance is contingent upon the type of disturbance and, more importantly, that the conditional response has implications for system-wide C and N dynamics. In addition,

herbivore-damaged trees had higher foliar tannin concentrations than did mechanically-damaged trees in our experiment, suggesting a whole-plant differential response by oaks (C. J. Frost and M. D. Hunter, *unpublished data*).

Herbivore activity and soil C and N dynamics

Herbivore activity stimulated changes in soil C and N independent of frass deposition, which implicates a root-mediated reaction to herbivore activity. Unfortunately, the experiment was not designed to address the rhizosphere, and the data do not clearly differentiate between potential mechanisms. There are four mechanisms that might, independently or interactively, contribute to belowground C and N fluxes following aboveground herbivory independent of surface soil inputs: (1) root turnover, (2) increased root growth, (3) increased root activity (independent of growth and rhizodeposition), and (4) increased root rhizodeposition.

The effects of root turnover on soil nutrient dynamics are not well known (Eissenstat and Yanai 1997, Matamala et al. 2003), though herbivore-mediated root turnover and resulting microbial-mediated decomposition can occur when herbivory hinders a plant's ability to sustain fine-root biomass, which die and are colonized by microbial decomposers. Ruess et al. (1998) demonstrated such a mechanism following mammalian browsing in the Alaskan taiga. In our system, this mechanism seems unlikely because soil respiration remained positively correlated with total leaf area following treatments and total soil N declined in herbivore-damaged systems.

Alternatively, aboveground damage might stimulate root growth, exploration, and biomass accumulation, as suggested by the deceleration-effect hypothesis (Ritchie et al. 1998). Increased root activity can alter soil respiration and N dynamics without adding root biomass. For example, roots can actively increase kinetic rates of nutrient uptake. Ion transport is an energetic process (Clarkson 1985), with nitrate assimilation requiring an estimated 20% of net primary production (Bloom et al. 1992). In our experiment, reduction in total soil N and C in herbivore-damaged systems supports these hypotheses.

Finally, rhizodeposition of C-rich compounds can provide a substrate for microbial activity that can result in a positive feedback of N mineralization and subsequent plant uptake in nutrient-rich soils (Hamilton and Frank 2001). Soil microorganisms are often limited by the quantity and quality of rhizo-deposited C from plant roots (Cheng et al. 1996, Knops et al. 2002), and rhizo-deposited C influences belowground nutrient dynamics (McNaughton et al. 1988, Cheng 1996, Frank and Groffman 1998, Kuzyakov and Cheng 2001, Kuzyakov et al. 2001, Cardon et al. 2002, Farrar et al. 2003). The reduction in total soil N and the increase in soil DOC following herbivore activity supports this hypothesis. Understanding the root-mediated effects of herbivory in forests and distinguishing between the competing mechanisms will be important for our understanding of the relationship among foliar herbivory, root dynamics, and ecosystem processes in temperate forests.

Conclusions

This study factorially manipulated herbivore damage (real and simulated) and subsequent frass deposition to test the hypothesis that frass deposition would increase aqueous export of N from soil independent of damage. While the data supported this hypothesis, herbivore damage also affected belowground N pools independent of frass additions. Statistical interaction between herbivore damage and frass additions seldom occurred, suggesting that herbivory and frass deposition have significant, but largely independent, effects on soil processes. The feeding activity of insect herbivores, even at endemic population densities, can therefore have direct and indirect effects on the cycling of C and N within the season of defoliation.

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