Responses of soil respiration, soil nutrients, and litter decomposition to inputs from canopy herbivores

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Abstract

We tested whether inputs from canopy herbivores would affect soil processes such as respiration, nutrient cycling, and decomposition along an elevation gradient. The five treatments we used were frass additions, throughfall additions, removal of all litter that fell during the study, removal of greenfall that fell during the study, and controls. Soil respiration was significantly reduced on low and mid elevation sites in litter exclusion, greenfall exclusion and throughfall addition treatments (from 0.846 g CO$_2$/m$^2$/h for controls to 0.618, 0.667, and 0.708 g CO$_2$/m$^2$/h, respectively, for the three treatments). Throughfall additions containing PO$_4$ and NH$_4$ contributed to significant increases in PO$_4$ (as much as 0.737 mg/l in 100 ml KCl extract greater than controls), but decreases in NO$_3$, (0.306 mg/l in 100 ml KCl extract less than controls), in soil solution samples compared to controls. We observed no significant treatment effects on litter decomposition. Precipitation and temperature influenced soil respiration, but both factors showed a significant interaction with elevation. Phosphate concentrations in soil solutions differed significantly with elevation (low elevation mean 0.097 mg/l, mid elevation mean 0.192 mg/l). Elevation had no significant effect on decomposition. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Canopy herbivory; Decomposition; Elevation gradient; Frass; Soil respiration; Throughfall

1. Introduction

Ecological research in the forest canopy has become an essential component of ecosystem ecology. The importance of the canopy as the interface between the atmosphere and the forest, and as the site of most photosynthesis in the forest, has become widely recognized (Parker, 1989). As access techniques for canopy studies have improved, research has expanded from descriptive to more quantitative studies, such as those on levels of insect herbivory (Reynolds and Crossley, 1995; Lowman and Wittman, 1996; Reynolds and Crossley, 1997). Insect herbivory in the canopy can have a major impact not only on the canopy itself, by removal of leaf tissue, but on forest floor processes such as decomposition and nutrient cycling, due to inputs from canopy herbivores (Schowalter et al., 1991; Reynolds et al., 2000). However, investigations of these links between the canopy and the forest floor is in its infancy (Lowman and Wittman, 1996).

In contrast with canopy research, investigations of vital processes taking place on the forest floor have been carried on for many years (Swift et al., 1979). The three processes of decomposition, soil respiration and nutrient cycling are of the utmost importance in understanding soil systems because they "...are integrating variables. They are generalized measurements of the functional properties of ecosystems, and they summarize the combined actions of soil microflora, fauna, abiotic variables and resource quality factors" (Coleman and Crossley, 1996, p. 139).

Decomposition plays an integral role in the functions of ecosystems (Olson, 1963; Odum, 1969) and is now given equal status to photosynthesis (Heal et al., 1997). The reason decomposition is so important is that in most terrestrial ecosystems, the majority of net primary productivity enters the decomposition compartment as plant litter (Wardle and Lavelle, 1997). Although decomposition rates vary as a function of temperature, moisture, chemical composition of the litter (Schlesinger, 1991) and the nutrient status of the soil (Verhoeven and Toth, 1995), soil biota play an integral role in the decomposition process as summarized by Seastedt (1984) and Moore et al. (1988) and, more recently, Wall and Moore (1999). Initial decomposition of organic material is performed primarily by microbes (Petersen and Luxton, 1982). After the material is colonized by bacteria and fungi, invertebrates such as arthropods...
physically break down the litter (comminute) and improve the abilities of microfauna (such as microarthropods and nematodes) to further comminute the litter (Hansen, 1999), feed on the microbes, and increase the cycling of nutrients (Lussenhop, 1992; Ettema, 1998; Yeates, 1998; Wall and Moore, 1999).

Decomposition is frequently measured using litter bags containing known amounts of litter (Crossley and Hoglund, 1962). A set of litter bags can be sampled over time and their weight loss serves as an index of decomposition. The litter bag technique has limitations, such as ignoring the fate of material leaving the bag, different microclimatic conditions within the bags compared to outside the bags, using fewer species of litter than occur together naturally, and excluding certain fauna. However, litter bags can be a very useful tool in decomposition studies as long as these limitations are recognized and other, more sensitive measurements, such as respiration and mineralization, are made concurrently (Heal et al., 1997).

Carbon dioxide fluxes from the soil and litter on the soil surface are an important component of the global terrestrial carbon cycle. Measurements in the field of CO₂ fluxes provide an estimate of the total respiration in the soil, which includes contributions of respiration from organic matter decomposition, soil fauna, and root respiration. Most of the production of CO₂ occurs in the surface litter where decomposition takes place quickly and a large proportion of the fine root biomass is found (Schlesinger, 1991).

Plants obtain many of the nutrients necessary for growth from the recycling of nutrients within the soil. Nutrient cycling in the soil is closely allied with decomposition, since most of the annual nutrient requirements of terrestrial plants come from the decomposition of organic matter in the soil (Schlesinger, 1991). A useful procedure for measuring availability of soil nutrients to plants is the resin bag technique (Binkley, 1984; Binkley et al., 1986). Bags containing positively and negatively charged resins are placed in the soil, where they take up anions and cations, respectively. Extracts of these resins can then be analyzed for such vital nutrients as PO₄−P, NO₃−N and NH₄−N. The resin bag technique has limitations; high nutrient availability values could result from any combination of high net mineralization rates, high ion mobility, and high water flow (Binkley, 1984).

Another current topic in ecological research is the effects of spatial variation on ecological processes (Kareiva, 1994). Variation in plant secondary compounds has been correlated with elevation differences (Louda and Rodman, 1983) as have differences in canopy arthropod density and canopy herbivory (Reynolds and Crossley, 1997). If canopy herbivores have a significant impact on soil processes, we will need to take such spatial variation into account.

Forests in mountainous areas are ideal settings for studying the interactions between spatial variation (along an elevation gradient) and effects of canopy herbivory on forest floor processes. The purpose of our study was to investigate the effects of inputs from canopy herbivores on forest floor biota and processes along an elevation gradient. Inputs from canopy herbivores include frass (excreta), throughfall (precipitation which has fallen through the canopy and been modified by the activity of canopy herbivores), and greenfall (portions of green leaves which fall due to insect herbivory). Insect frass and throughfall are known to contain nutrients which could stimulate nutrient cycling and decomposition (Schowalter et al., 1991; Lovett and Ruesink, 1995; Eshleman et al., 1998; Reynolds et al., 2000). Greenfall is also nutrient-rich and has been proposed as an important source of nitrogen during the growing season for forest floor processes (Risley and Crossley, 1988, 1992). A separate paper (Reynolds et al., 2001) provides information on the rates of litter decomposition and abundance of microarthropods and nematodes along an elevation gradient. It also includes data from a manipulative experiment in which we modified canopy herbivore inputs (frass, throughfall and greenfall) and leaf litter biomass to assess their effects on the abundances of soil microarthropods and nematodes. The present paper includes information from our manipulative experiment in which we measured the responses of soil respiration, soil nutrients, and litter decomposition to inputs from canopy herbivores. The purpose of this paper is to provide evidence that inputs from canopy herbivores can influence soil processes such as respiration, decomposition, and nutrient cycling.

2. Materials and methods

2.1. Study site

This study was conducted at the Coweeta Hydrologic Laboratory, operated by the US Forest Service. Coweeta is in the Nantahala Mountain Range of western North Carolina, within the Blue Ridge Physiographic Province at latitude 35° 03’N and longitude 83° 25’W (Swank and Crossley, 1988). Our three sites within Coweeta have similar aspects and vegetation but range in elevation from 800 m (low) through 1000 m (middle) to 1350 m (high) (Reynolds and Crossley, 1995). Classification of soils includes Typic Hapludults (low elevation), Typic Dystrochrepts (mid elevation) and Typic Haplubrepts (high elevation) (Knoepp and Swank, 1998). Precipitation measurements are made weekly at eight standard rain gauges in the Coweeta basin (Swift et al., 1988). Precipitation levels used in our soil respiration analysis were averaged from two stations closest to our study sites.

2.2. Experimental design

Twenty-five 1 m² quadrat boxes, constructed of untreated pine wood, were positioned on each elevation site. Tops were also made of pine but covered with 1-cm mesh plastic bird netting. Twenty of the boxes were adjacent to
20 sampling stations previously used to estimate inputs of frass, greenfall and throughfall (Reynolds et al., 2000). Five more were placed in additional randomly selected spots so that the 25 boxes were within a circle of diameter 40 m. Five replicates of each of five treatments were placed at each elevation. The treatments were frass additions, throughfall additions, removal of litter that fell during the study, removal of greenfall that fell during the study, and control. The frass used for this study was collected during the previous year from caged specimens of walking sticks (Anisimorpha buprestoides (Stoll)), forest tent caterpillars (Malacosoma disstria Hübner) and spiny oakworm caterpillars (Anisota sp.). Walking sticks and caterpillars were fed Rhododendron maximum L. and Quercus rubra leaves, respectively, both of which are dominant members of the flora at Coweeta. Frass was brushed out of the plastic cages daily and held at -13.0°C. until shortly before application. All the frass was carefully mixed before the initial weighing.

We chose the quantities of frass and throughfall to add to our treatments from measurements made at each elevation during the previous 2 years (Reynolds et al., 2000). From 20 frass and throughfall collectors at each elevation, we estimated (a) average weekly frass deposition and (b) average monthly N and P concentrations of throughfall. We used these data to double the average frass and throughfall nutrient inputs into our treatments and to reflect seasonal variation in inputs. Doubling these inputs is well within the range of natural variation observed previously at Coweeta (Reynolds et al., 2000). The amount of frass applied to each frass treatment plot varied between 2.9 and 14.3 g (dry weight) m\(^{-2}\) week\(^{-1}\), depending on the time of year (Fig. 1). Artificial throughfall was generated by dissolving NH\(_4\)Cl and KH\(_2\)PO\(_4\) in deionized water. These two ions were used because we estimated that the treatment sites were already receiving naturally occurring throughfall containing many nutrients, including NH\(_4\)-N and PO\(_4\)-P. Ammonium concentrations added ranged from 7.3 to 224.0 mg m\(^{-2}\) week\(^{-1}\) and PO\(_4\)-P concentrations were 0.7 to 36 mg m\(^{-2}\) week\(^{-1}\) (Fig. 2). The same volume of solution, 800 ml, was used on each throughfall plot. Control plots only were sprinkled with 800 ml of deionized water. Litter exclusion was chosen as one of our treatments to compare the relative effects of herbivore inputs and leaf senescence on soil invertebrates and nutrient dynamics. Greenfall exclusion was used rather than greenfall additions because it was easier than collecting and adding greenfall from additional collectors. Litter and greenfall were removed from the mesh over litter boxes at least once a week. For controls, frass, and throughfall treatments, litter which fell on top of the mesh was spread over the litter inside the box at least weekly.

2.3. Litter decomposition, soil respiration and soil nutrients

The three variables we measured as responses to canopy inputs were litter decomposition, soil respiration, and nutrient concentration of soil solutions. We used litter bags (Crossley and Hoglund, 1962) to measure mass loss and decomposition rates. In October of 1996 we collected fresh litter from Q. rubra L. (red oak) and Acer rubrum (L.) at Coweeta. Leaves were then air-dried in the laboratory. Leaves were dried so that the initial weights of leaves in the litter bags would not include varying amounts of moisture. These species were chosen because they are common at our study sites and were used in a previous study of variation in canopy herbivory (Reynolds and Crossley, 1997). We put approximately 1 g of A. rubrum and 1.5 g of Q. rubra into each litterbag, then recorded the initial weight of the leaves. Litterbags were made of nylon fish net with a mesh size of 1.5 mm and were 15 × 15 cm. After the leaves were put in the bags, the bag was stapled shut with a plastic, numbered tag attached. Two litterbags

![Fig. 1. Frass added each month (g/m\(^2\)), to treatment boxes along an elevation gradient at Coweeta Hydrologic Laboratory, 1998. Within each month, equal amounts of frass were added each week.](image-url)
were retrieved from each even-numbered quadrat every other month, and two litterbags were retrieved from odd-numbered quadrats on the alternate months. Each pair of litterbags was sealed in a plastic bag before transportation to our laboratory. One litterbag from each collection was used for sampling microarthropods; the dried litter was then weighed to determine mass loss. Exponential decay constants (k values: Olson, 1963) were calculated based on these dry weights of litter. The other litterbag was extracted for nematodes (Reynolds et al., 2001).

Soil respiration measurements were made with a PP Systems EGM-2 Environmental Gas Monitor (PP Systems, Haverhill, MA, USA). This instrument uses a non-dispersive infrared measurement technique combined with a soil respiration chamber (Parkinson, 1981). A soil temperature probe (STP-1) was coupled to the EGM-2. We made measurements of soil temperature, at a depth of approximately 5 cm, with every respiration measurement. Soil respiration measurements were begun on 12 May 1998 and done approximately twice a month through 13 October 1998. Ten sets of measurements were made. Because the battery could not hold a charge for the length of time it took to measure all 75 quadrats in a day, and because the instrument was not designed for quick battery changes in the field, respiration measurements were done over 2 consecutive days.

Pairs of ion exchange resin bags, positively and negatively charged resin contained in lengths of nylon stockings (Binkley, 1984; Binkley et al., 1986), were placed in the soil approximately 5 cm deep in each of the quadrat boxes. Each bag was approximately 16 cm$^2$ and contained 10 g of resin. Resin bags were initially installed in early April, and then replaced with fresh resin bags every other month until December 1998. Therefore, there were four resin bag collections. The contents of the resin bags were extracted in 100 ml of 1 M KCl and analyzed for NO$_3$-N, NH$_4$-N, and PO$_4$-P using the automated cadmium reduction, phenate, and automated ascorbic acid reduction methods respectively (Greenberg et al., 1992) on an Alpkem Flow-Injection Analyzer in the Institute of Ecology Analytical Chemistry Laboratory.

Twenty-four litterbags were placed in each quadrat in April 1997. Litter and greenfall removal were begun a week later and continued through September 1998. Frass

Fig. 2. (a) NH$_4$-N (mg/m$^2$), and (b) PO$_4$-N (mg/m$^2$), monthly additions to treatment boxes along an elevation gradient at Coweeta Hydrologic Laboratory, 1998. The same amount of nutrient was added each week for a particular month.
Fig. 3. Effects of treatments on soil respiration (g of CO₂ per m² per hour) averaged for May–October 1998, for low and middle elevations at Coweeta Hydrologic Laboratory. Treatments were control, litter exclusion (litter ex), greenfall exclusion (greenfall ex), doubling throughfall nutrients (thrufall ad), and doubling frass input (frass ad). Error bars are included for visual reference. Since the data were not normally distributed, they were analyzed using non-parametric procedures.

and throughfall additions were begun 5 May and 11 May, respectively, in 1998 and continued weekly through September 1998.

Results from our input manipulation study are reported only for the low and mid elevation sites, since an outbreak of the sawfly Periclista sp. (Hymenoptera: Tenthredinidae) at the high elevation site added large quantities of frass to all quadrat boxes, compromising the treatments. The consequences of this sawfly outbreak on soil processes are reported elsewhere (Reynolds et al., 2000).

2.4. Data analysis

Decay constants were calculated by regressing the log of % litter remaining against date collected (Olson, 1963). Data were then analyzed using ANOVA and Tukey’s Studentized Range (HSD) Test (SAS 6.12, 1996). The data for soil respiration and nutrients in resin bags were not normally distributed; therefore the effects of the treatments on these parameters were analyzed using the GLIM Genmod Procedure of SAS 6.12 (1996). Since this procedure cannot be used to compare differences among treatments, we ran a Tukey’s test on respiration and nutrient data for comparison purposes only.

3. Results

While the Proc Genmod procedure indicates that rates of soil respiration differed among treatments \((\chi^2 = 17.92, df = 4, P = 0.0013, \text{Fig. 3, Table 1})\), it does not allow direct comparisons among treatment means. A parametric Tukey’s Studentized Range (HSD) Test suggests that soil respiration in control and frass additions plots was significantly greater than in litter exclusion plots (Table 4). However, our data break the assumptions of the Tukey’s Test and we present those results for comparison purposes only. In general, soil respiration increased with soil temperature [Fig. 4(a)]. The mid elevation site usually had the highest soil respiration for a given temperature. However, the slope of the relationship between temperature and respiration varied between elevations, demonstrating a significant interaction between soil temperature and soil respiration (ele*temp \(\chi^2 = 5.49, df = 1, P = 0.0191, \text{Table 1})\). Soil respiration increased slightly with increased precipitation during the previous week [Fig. 4(b)]. Again, the slope of the relationship between soil respiration and precipitation varied between elevations (ele*ppt \(\chi^2 = 20.27, df = 1, P < 0.0001, \text{Table 1})\).

The average \(k\) value (day⁻¹) for decomposition of litter in litter bags was not significantly different \((F = 1.07, P = 0.308, n = 50)\). Also, we did not observe any treatment effect (treatment \(F = 1.19, P = 0.330, n = 50, \text{Table 2})\).

The average concentrations of PO₄-P in resin bag

<table>
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<th>Log-likelihood</th>
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<th>P</th>
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<td>0.0343</td>
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<td></td>
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Fig. 4. Effects of temperature and elevation (a) and precipitation (from the week prior to CO$_2$ measurement) and elevation (b) on soil respiration (g of CO$_2$ per m$^2$ per hour) at Coweeta Hydrologic Laboratory, 1998.

Table 2
Average $k$ value (day$^{-1}$) for decomposition of litter in litter bags at the Coweeta Hydrologic Laboratory, NC for two years. Data were analyzed using ANOVA, means were compared using Proc Means (SAS 6.12). Treatments were litter exclusion, greenfall exclusion, frass additions, throughfall additions, and control.

<table>
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<tr>
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<tr>
<td>Litter exclusion</td>
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<tr>
<td>Greenfall exclusion</td>
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<tr>
<td>Frass additions</td>
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<tr>
<td>Throughfall additions</td>
<td>– 0.0341</td>
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<td>Control</td>
<td>– 0.0388</td>
</tr>
<tr>
<td>Elevation 2</td>
<td></td>
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<tr>
<td>Average</td>
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<tr>
<td>Litter exclusion</td>
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<td>Greenfall exclusion</td>
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</tr>
<tr>
<td>Frass additions</td>
<td>– 0.0405</td>
</tr>
<tr>
<td>Throughfall additions</td>
<td>– 0.0403</td>
</tr>
<tr>
<td>Control</td>
<td>– 0.0459</td>
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</tbody>
</table>

extracts from the mid elevation site were greater than those from the low elevation site ($\chi^2 = 6.471, df = 1, P = 0.011$, Fig. 5, Table 3). Throughfall additions increased the concentrations of PO$_4$–P in resin bags for the first three collections [Fig. 6(a)–(c)]. By October–November, after the last throughfall addition in late September, litter exclusion, frass additions, and throughfall addition treatments had the lowest levels of PO$_4$–P in their resin bags ($\chi^2 = 10.087, df = 4, P = 0.039$, Fig. 6(d), Table 3). Although this interaction term indicates that the role of treatment on PO$_4$–P varied over time, the effect of treatment was substantial ($P = 0.0001$, Table 3). Therefore, we ran a Tukey’s Studentized Range (HSD) Test to compare the means of the treatments (Table 5). The results suggested that the average concentration of PO$_4$–P in resin bags from throughfall treatments was significantly greater than the average concentration of PO$_4$–P from litter exclusion treatments. Again, since our data were not normally distributed, they break the assumptions of the Tukey’s Test, and the Tukey results are reported for comparison purposes only.

Resin bags from the litter exclusion treatments had the
Fig. 5. Effects of elevation on average soil PO₄-P (mg/l in 100 ml 1 M KCl extracts of resin bags) at Coweeta Hydrologic Laboratory, 1998. Error bars are included for visual reference only, and represent the standard error of the mean. Since the data were not normally distributed, they were analyzed using non-parametric procedures.

Table 3
Effects of date, elevation, and experimental treatments on ion concentrations from resin bags (100 ml of 1 M KCL extracts) at the Coweeta Hydrologic Laboratory, NC. Data were analyzed using GLIM. ele, Elevation; trt, treatment. Treatments were litter exclusion, greenfall exclusion, frass additions, throughfall additions, and control. The model presented is the most parsimonious using the methods of Agresti (1996)

<table>
<thead>
<tr>
<th>Ion</th>
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<th>Terms</th>
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<th>df</th>
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highest concentrations of NO₃⁻-N compared to the other treatments [Fig. 7(a)]. While Proc Genmod indicates that the effects of treatment on NO₃⁻-N varied (treatment $\chi^2 = 10.44, df = 4, P = 0.0336$, Table 3), it does not allow direct comparisons among treatment means. A parametric Tukey's Studentized Range (HSD) Test suggests that average NO₃⁻-N concentrations in resin bags were significantly greater in litter exclusion treatments than in throughfall treatments (Table 4). Since our data break the assumptions of the Tukey's Test, we present these results for comparison purposes only. The average NO₃⁻-N values were lowest in the October–November collections [date $\chi^2 = 6.761, df = 1, P = 0.0093$, Fig. 7(b), Table 3]. We measured no significant effects on NH₄⁺-N in resin bags among treatments, dates or between elevations.

4. Discussion

4.1. Soil respiration

The reduction in soil respiration following litter exclusion (Fig. 3) is not surprising. Litter provides a major source of carbon for soil respiration (Brady and Weil, 1996) and may also contribute to a microclimate that favors decomposers. We have noted that oribatid and prostigmatid mite numbers were reduced in these same litter exclusion treatments (Reynolds et al., 2001). We attribute the reduction in respiration either to a direct effect—the harsher microclimate and/or an indirect effect—resource limitation which may have developed in quad rat boxes as the original litter decomposed and no more litter fell. The apparent reduction in soil respiration following greenfall exclusion may indicate that greenfall provides a significant nutrient resource for soil flora, fauna and/or roots.

We observed no apparent effect on soil respiration from our frass additions (Fig. 3, Table 1). Lovett and Ruesink (1995) reported increased carbon mineralization rates (CO₂ evolution) from soil microcosm samples treated with frass. Although it is difficult to compare the relative amounts of frass and soil between a microcosm and a field experiment, it appears that Lovett and Ruesink added a greater amount of frass in proportion to their soil than we did. Their treatments were designed to mimic outbreak conditions whereas ours were typical of endemic insect densities.

We also observed a reduction in soil respiration following throughfall additions (Fig. 3). No change in respiration would imply that the nutrient ions remained mobile and left the soil system quickly or were adsorbed onto soil particles, since uptake by roots or soil microbes should have resulted in increased soil respiration. However, NO₃⁻-N in resin bag extracts decreased in throughfall treatments [Fig. 7(a)], even though PO₄-P in resin bag extracts increased in all throughfall treatments during the growing season (Fig. 6). Since NO₃⁻-N from resin bag extracts decreased, we think that some form of biological uptake of NO₃⁻-N occurred. We hypothesize that mycorrhizal fungi took up the NO₃⁻-N, quickly and efficiently, leaving soil microbes unable to use the PO₄-P even though PO₄-P...
is limiting in low elevation Coweeta soils (Wallbridge et al., 1991; Wright and Coleman, 1999). Thus, the reduced respiration we observed in throughfall treatments could be due to decreased growth of soil microbes as they were out competed by mycorrhizal fungi, which are thought to have lower CO₂ production when assimilating mineral nitrogen than free-living soil microbes (Aber et al., 1998). We realize this hypothesis implies that NO₃-N is limiting in our low and mid elevation sites, which may seem contrary to suggestions of previous authors (Swank and Vose, 1997) that reference watersheds at Coweeta may be in a transition phase between stage 0 and stage 1 of nitrogen saturation as proposed by Aber et al. (1989). However, NO₃-N concentrations in reference streams at Coweeta are still low, especially for the low elevations (Swank and Vose, 1997), therefore low elevation soils may still be nitrogen limited.

4.2. Soil nutrients

The lower levels of PO₄-P in resin extracts at our low elevation site (Fig. 5) may indicate greater uptake by plant roots, soil microbes or P-sorbing minerals. It has been reported (Wallbridge et al., 1991) that these three factors reach their maximal levels at Coweeta in the near surface mineral horizons of watersheds 1 and 18 (where our low elevation site is located). As Wright and Coleman (1999) pointed out, severe limitations on available P would cause immediate uptake of any mineralized P forms, thus quickly removing them from the soil solution.

Although the role of treatment on PO₄-P in resin extracts varied over time, our results suggest that the average concentration of PO₄-P in resin bags from throughfall treatments was significantly greater than in bags from litter exclusion treatments (Tables 3 and 5, Fig. 6). This effect is most apparent early in the growing season [Fig. 6(a)], when cooler soil temperatures may have inhibited biological uptake of excess PO₄-P. As soil temperatures increased over the summer, more uptake of PO₄-P from throughfall is apparent [Fig. 6(b) and (c)]. By October–November, amounts of PO₄-P in throughfall treatments are minimal.
[Fig. 6(d)], even though inputs, at least for the mid elevation sites [Fig. 2(b)] are comparable to early season PO$_4$-P inputs. This suggests to us that biological activity in the soil, stimulated by fresh litterfall, has peaked and nutrient uptake is occurring (Lovett and Ruesink, 1995).

The effects of greenfall exclusion on PO$_4$-P and NO$_3$-N in resin bags were not significant [Figs. 6 and 7(a), Tables 4 and 5]. This could mean that any PO$_4$-P leached from greenfall in controls was immediately taken up, either by plant roots or soil microbes, or that P compounds are more tightly bound in greenfall, and effects from greenfall exclusion would not be apparent during the course of this experiment. These ideas are not mutually exclusive. Since we have some indication that soil respiration was reduced in greenfall exclusion plots (Fig. 3), we believe that some biological uptake of PO$_4$-P occurred in the controls.

We observed greater average concentrations of NO$_3$-N in resin extracts from the litter exclusion treatments than in the controls [Fig. 7(a)]. We think that this is because the litter exclusion treatments had reduced the numbers or activity of soil microbes, as shown by reduced respiration in litter exclusion treatments (Fig. 3) and, therefore, less uptake of NO$_3$-N occurred in the litter exclusion treatments. Average NO$_3$-N in resin extracts was lower for the October–November collection [Fig. 7(b)] than the other three collection dates. As with PO$_4$-P, we think that increased input of fresh litter during autumn may have led to immobilization of nitrogen compounds as soil microbes received a new source of carbon (Lovett and Ruesink, 1995).

Any PO$_4$-P or NO$_3$-N in frass was apparently immobilized in some fashion, perhaps by soil microbes as suggested

Table 4

Effects of treatments on soil respiration (g of CO$_2$ per m$^2$ per hour) and soil NO$_3$-N (mg/l in 100 ml 1 M KCl extracts of resin bags) averaged for May–October, 1998, for low and middle elevations at Coweeta Hydrologic Laboratory. Treatments were: control, litter exclusion (litter ex), greenfall exclusion (greenfall ex), doubling throughfall nutrients (thrufall ad), and doubling frass input (frass ad). Error terms are included for comparison purposes only. Since the data were not normally distributed, they were analyzed using non-parametric procedures.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>g CO$_2$/m$^2$/h (±SE)</th>
<th>NO$_3$-N (±SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>0.846 (0.064)</td>
<td>0.921 (0.146)</td>
</tr>
<tr>
<td>Litter ex</td>
<td>0.618 (0.049)</td>
<td>1.232 (0.154)</td>
</tr>
<tr>
<td>Greenfall ex</td>
<td>0.667 (0.056)</td>
<td>0.762 (0.143)</td>
</tr>
<tr>
<td>Thrufall ad</td>
<td>0.708 (0.055)</td>
<td>0.615 (0.095)</td>
</tr>
<tr>
<td>Frass ad</td>
<td>0.874 (0.063)</td>
<td>0.797 (0.153)</td>
</tr>
</tbody>
</table>
Fig. 7. Effects of treatments (a) and dates (b) on average soil NO$_3$-N (mg/l in 100 ml 1 M KCl extracts of resin bags) at Coweeta Hydrologic Laboratory, 1998. Treatments were control, litter exclusion (litter ex), greenfall exclusion (greenfall ex), doubling throughfall nutrients (thrufall ad), and doubling frass input (frass ad). Error bars are included for visual reference only, and represent the standard error of the mean. Since the data were not normally distributed, they were analyzed using non-parametric procedures.

by Lovett and Ruesink (1995), since the amounts of these nutrients in resin bag extracts were either lower [Fig. 6(b) for PO$_4$-P] or no different between frass additions and controls [Fig. 6(a), (c), and (d) for PO$_4$-P; 7(a) for NO$_3$-N].

Average NO$_3$-N concentrations in resin bags from throughfall addition plots appear to be lower than in controls [Fig. 7(a)]. This suggests that addition of labile nutrients stimulated biological processes, and increased uptake of NO$_3$-N. Since date had a stronger effect than treatment (Table 3), it is probable that the increased nutrient uptake in October–November [Fig. 7(b)] was again very influential.

4.3. Precipitation, soil temperature and soil respiration

Although our analyses indicated an interaction between temperature and elevation on soil respiration (Table 1), the pattern of increased soil respiration with soil temperature was apparent at both sites [Fig. 4(a)], and is similar to that

<table>
<thead>
<tr>
<th>Treatment</th>
<th>April–May</th>
<th>June–July</th>
<th>August–September</th>
<th>October–November</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter ex</td>
<td>0.002 (0.002)</td>
<td>0.030 (0.023)</td>
<td>0.061 (0.030)</td>
<td>0.032 (0.02)</td>
</tr>
<tr>
<td>Green ex</td>
<td>0.044 (0.027)</td>
<td>0.229 (0.124)</td>
<td>0.035 (0.016)</td>
<td>0.202 (0.129)</td>
</tr>
<tr>
<td>Frass ad</td>
<td>0.075 (0.053)</td>
<td>0.107 (0.087)</td>
<td>0.078 (0.025)</td>
<td>0.015 (0.007)</td>
</tr>
<tr>
<td>Thrufall ad</td>
<td>0.778 (0.630)</td>
<td>0.557 (0.275)</td>
<td>0.209 (0.164)</td>
<td>0.010 (0.006)</td>
</tr>
<tr>
<td>Control</td>
<td>0.041 (0.023)</td>
<td>0.313 (0.129)</td>
<td>0.060 (0.018)</td>
<td>0.084 (0.072)</td>
</tr>
</tbody>
</table>
found in other forests in the southeastern United States (Hanson et al., 1993). A second pattern was also noticeable: in general, respiration was greater at the mid elevation site than at the low elevation site. We reported elsewhere a similar pattern for the density of microarthropods in litter bags and greater rates of decomposition at higher elevations along the gradient (Reynolds et al., 2001. See also Hoover and Crossley, 1995). Overall, higher elevation sites at Coweeta appear to be characterized by increased rates of decomposition and soil respiration, and higher densities of soil fauna (Hoover and Crossley, 1995). Our explanation for these phenomena was that the microarthropods were tracking the increased abundance of microbial decomposers which we assumed were greater where decomposition was greater. Increased soil respiration at the higher site is consistent with our hypothesis.

Over most of the range in precipitation observed during our study, soil respiration was higher at mid elevation than at low elevation [Fig. 4(b)]. Again, this is consistent with our findings that decomposition was also greater at higher elevations, and was probably due to higher densities of soil microbes which were actively decomposing (Reynolds et al., 2001. See also Hoover and Crossley, 1995).

4.4. Litter decomposition

Although we measured significant differences in decomposition between the low and mid elevation site in a previous study using the same two species of litter (Reynolds et al., 2001), we did not detect any differences in rates of decomposition between the two sites in our experiment. Litter in the present study was set out in April 1997 and followed through February 1999. In our previous study, bags were set out in December 1996 and followed through 15 December 1998. It is possible that differences in microclimate between the two sites for these different time periods could have affected decomposition rates.

Why are there no differences among the treatments in decomposition of litter in bags? This is surprising, because we did see differences among treatments in factors related to decomposition such as microarthropod numbers (Reynolds et al., 2001) and respiration (reported here). Perhaps over the 2 years of this litterbag study, differences that might have occurred over shorter intervals (such as the first spring and summer when biological activity usually causes increases in decomposition, Coleman and Crossley, 1996) were obscured. Also, the lack of significant treatment effects may be a result of not initiating the throughfall and frass treatments until the litter had been in place for over 1 year. We acknowledge that the litterbag technique is subject to several sources of error, such as exclusion of macrofauna and microclimatic differences between litter in litterbags and ‘free’ litter (Coleman and Crossley, 1996). However, we maintain that the technique is a valuable tool for comparative studies.

5. Conclusion

In this experiment, we were testing whether inputs from canopy herbivores would affect the critical soil processes of respiration, nutrient cycling, and decomposition. We observed significant effects on soil respiration from litter exclusion, greenfall exclusion, and throughfall additions. All three treatments caused reduced soil respiration on both low and mid elevation sites. We measured no significant effect from our treatments, nor from elevation differences, on litter decomposition. We hypothesize that the timing of treatment applications, some of which were in the second year of the decomposition study, may have affected our results. Throughfall additions had opposite effects on NO3–N and PO4–P, and were not entirely consistent with the effects measured on soil respiration. We think the explanation may be due to activities of mycorrhizal fungi taking up nitrate and thus outcompeting soil microbes, which were then unable to use the PO4–P. We can say that soil respiration and soil nutrient cycling showed significant responses to some of our experimental inputs from canopy herbivores. In conjunction with data presented in a separate paper (Reynolds et al., 2001), these experiments have provided strong evidence for the importance of inputs from canopy herbivores on soil processes.

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