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Carbon and nitrogen mineralization from decomposing gypsy moth frass

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Abstract Defoliation of forests by insects is often assumed to produce a pulse of available nitrogen (N) from the decomposition of frass pellets. In this study we measured rates of carbon (C) and N mineralization from gypsy moth frass incubated with and without soil, and for soil alone. Incubations were at constant temperature and soil moisture conditions and lasted for 120 days. We found that gypsy moth frass contains much labile C as well as extractable N, and that the stimulation of microbial growth by the labile C results in immobilization of essentially all of the extractable N in the frass. The response of the microbes is fast, beginning within 1 day and lasting at least 90 days. This immobilization response represents an efficient mechanism for conserving N within a forest ecosystem after a defoliation event.

Key words Gypsy moth · Frass · *Lymantria dispar* · Nitrogen cycle · Nitrogen mineralization

Introduction

Defoliation of a forest by phytophagous insects represents a severe perturbation to the nitrogen (N) cycle, in that the substantial quantity of N in foliar biomass is transferred abruptly to the forest floor, and the trees are denied the possibility of internally recycling N by resorption from the foliage prior to senescence (Carlisle et al. 1966; Schowalter et al. 1986, 1991; Hollinger 1986). It is commonly assumed that N availability in forest soils is increased by the deposition of N-rich and readily decomposable pellets of insect excrement (frass). This increased availability of N could lead to stimulation of plant growth (e.g., Mattson and Addy 1975; Schowalter 1981), or to increased loss of N from the ecosystem if plant or microbial uptake is not sufficient to retain the mobilized N (Swank et al. 1981).

The assumption of increased N availability requires (1) that significant quantities of N be returned to the forest floor as frass, and (2) that the N in the frass is readily mineralizable, presumably more so than the N in senescent foliage. The first of these points has substantial support in the literature. In forests undergoing attack by defoliating insects, nitrogen return in frass litterfall can be substantial, often greater than N return in senescent leaf litter. For instance, Fogal and Slansky (1985) reported that N return in frass exceeded N return in needle litter for a Scots pine forest which was 75–85% defoliated by the European sawfly. In a mixed oak forest in Pennsylvania, N return in gypsy moth frass was greater than in leaf litterfall, despite considerable reflushing of leaves after the early-summer defoliation (Grace 1986). For deciduous and evergreen oak trees in California, Hollinger (1986) found that N return to the soil was up to twice as high in defoliation years as in non-defoliation years because of the inability of the trees to resorb N from the foliage during defoliation years.

The second point, that the N in frass is readily mineralizable, is often assumed (e.g., Gosz et al. 1972; Ohmart et al. 1983) but has not, to our knowledge, been explicitly tested in any forest ecosystem. The expectation appears to be that the frass has a high concentration of labile N and would therefore effectively fertilize a forest.

In this study, we measured the rates of potential carbon and nitrogen mineralization from the frass of the gypsy moth (*Lymantria dispar*, Lepidoptera: Lymantriidae) incubated in the laboratory, both with and without added soil. Our purpose was to determine the rates of potential N and C mineralization, their temporal pattern over the incubation period, and the fraction of frass N and C that were mineralized within this period.

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The gypsy moth, native to Eurasia, was introduced to North America near Boston in 1868 or 1869 (Forbush and Fernald 1896). Since that time it has spread throughout the eastern United States, and has currently extended its range as far south as Virginia and as far west as Michigan (USDA Forest Service 1994). It primarily attacks oaks (*Quercus*), although in outbreak periods when food is in short supply almost any foliage will be consumed. In the north-eastern United States, gypsy moth defoliations recur at approximately 8–10 year intervals, and the outbreak periods last 2–3 years (Doane and McManus 1981). During those periods, severely affected forests can suffer complete defoliation, usually in early summer, and broad areas of forest can experience at least some defoliation.

Methods

Sample preparation

Soil samples used in the carbon and nitrogen mineralization incubations were obtained from the surface soil (top 3–5 cm, excluding fresh litter) of an upland oak forest in the North Cannoo Hill area of Millbrook, New York. We collected the soil in mid-October 1993 from a single location to minimize heterogeneity. The soil was passed through an 8-mm sieve to remove stones and large roots and then de-ionized water was added to bring the sample to field capacity.

Frass was collected in June 1993 from laboratory-reared late instar gypsy moth caterpillars fed on black oak (*Quercus velutina*) foliage obtained from field-grown, mature trees. Frass was dried at 40 °C and stored until the beginning of the experiment (October 1993), at which time it was brought to 80% of its water holding capacity with deionized water. Frass and soil samples were analyzed for %C and %N using a C-N analyzer (Carlo-Erba NA1500), and for percentage of organic matter by ashing in a muffle furnace.

Carbon mineralization

Potential carbon mineralization was measured by incubating samples in glass quart (946 ml) canning jars. Four replicates of the following three treatments were employed: soil alone, soil + frass, and frass alone. We used 10.7 g soil and 2.1 g frass, corresponding to dry weights of 4.5 g and 1 g respectively. We suspended a damp filter paper within each jar to maintain high humidity in the headspace and prevent dessication of the soil and frass. Filters were re-wetted weekly throughout the experiment.

We measured C mineralization as CO_2 accumulation is sealed jars over 24 h. During the measurement period the jars were sealed with airtight lids fitted with butyl rubber septa. Headspace samples of 0.5 ml were extracted through the septum with a syringe and then analyzed for CO_2 concentration with a gas chromatograph (Shimadzu GC-8A). Measurements were made on days 0, 1, 2, 4, 7, 10, 20, 30, 60, 92 and 120 after the start of the experiment. In between the 24-h incubation periods the jars were covered with plastic film instead of the sealed lids, allowing gas exchange but minimizing loss of moisture. Samples were incubated in the dark at 21 ± 2 °C throughout the 120-day experiment.

Rates were expressed as micrograms C released per gram dry weight of substrate per day. In the calculations we accounted for the loss of dry weight through CO_2 evolution during the course of the experiments. We calculated net C mineralization for the frass in the soil + frass treatment by subtracting the mean net C mineralization in the soil alone treatments from that in the soil + frass treatments, and expressing the rate per gram dry weight of frass in the jars, as follows:

$$C_f = [(C_{sf}\mathrm{DW}_{sf}) - (C_s\mathrm{DW}_s)]\ \mathrm{DW}_f^{-1} \quad (1)$$

where C is the C mineralization rate per gram dry weight, DW is the dry weight, and the subscripts *s*, *sf*, and *f* refer to the soil, soil + frass, and the frass component of the soil + frass treatment, respectively. This value (labelled "frass calc" in Figures and Tables) is the best estimate of the effect of the frass on potential C mineralization from the soil + frass mixture. This effect includes mineralization of the C in the frass as well as any stimulation of soil C respiration caused by the presence of frass (soil "priming" effect, see Discussion).

Nitrogen mineralization

To measure potential net N mineralization we applied the same three treatments used for C mineralization: soil alone, soil + frass, and frass alone. We used 21.4 g soil and 4.3 g frass wet weight (corresponding to 9 g and 2 g dry weight, respectively) to maintain the same ratio of soil to frass as in the C-mineralization experiments while increasing absolute amounts of soil and frass, ensuring sufficient extractable N for analysis. Samples were placed in 120-ml plastic cups and covered with plastic film to prevent moisture loss. These samples were incubated in the dark alongside the C mineralization samples.

Four replicate samples of the soil and soil + frass treatments were incubated for periods of 0, 10, 20, 30, 60, 90, and 120 days, for a total of 56 samples. Four frass-only samples were incubated for 0, 30, and 90 days (12 samples); more time periods were not possible because of lack of sufficient frass for incubation. To extract the samples, 100 ml of 2 M KCl was added to the cups and allowed to stand for 18 h, after which the supernatant was decanted through a 4-ply filter of laboratory tissues (Kimwipes) and collected for analysis. Blank samples were obtained by decanting fresh extraction solution through the filters. Samples were treated with 1 drop of chloroform per 100 ml of sample and stored in the dark at 4 °C until chemical analysis could be performed. Solutions were analyzed for concentrations of NO_3^--N using the cadmium reduction method and NH_4^+-N using the indophenol blue method on an Alpkem auto-analyzer.

Potential net N mineralization was calculated as the accumulation of extractable $NH_4^+ + NO_3^-$ in the sample during the incubation period, expressed as micrograms of N (g dry weight)$^{-1}$ day^{-1}. Potential net nitrification was calculated as the accumulation of NO_3^- only, expressed in the same units. As for C mineralization, the calculations accounted for the loss of dry weight from the samples by CO_2 evolution during the course of the study. The potential net mineralization and nitrification of the frass in the soil + frass mixture was calculated by subtracting the total extractable NH_4^+ or NO_3^- for the soil alone treatment from that of the soil + frass treatment, and expressing the result per g dry weight of frass (as in Eq. 1). As discussed above for C mineralization, this "frass calc" value is the best estimate of potential net N mineralization and nitrification rates for frass supplied with nutrients and microbes from the soil.

For C mineralization, N mineralization and nitrification, treatment effects were tested by analysis of variance (SAS GLM procedure) for each time period, and individual treatment means were compared using the Ryan-Einot-Gabriel-Welsch multiple *F*-test (SAS 1985).

Results

The soil used in this experiment contained 18.4% C, 0.8% N, and 35.2% organic matter. The frass collected

from the laboratory-reared gypsy moth larvae contained 48.5% C, 2.4% N, and 94.8% organic matter. The N concentration of the frass was 60% higher than the 1.5% N measured for gypsy moth frass collected in unmanaged oak forests near Millbrook. This difference may be due to leaching or volatilization of N from frass before collection in the field, or perhaps to the different feeding conditions in the rearing cages compared to the forest.

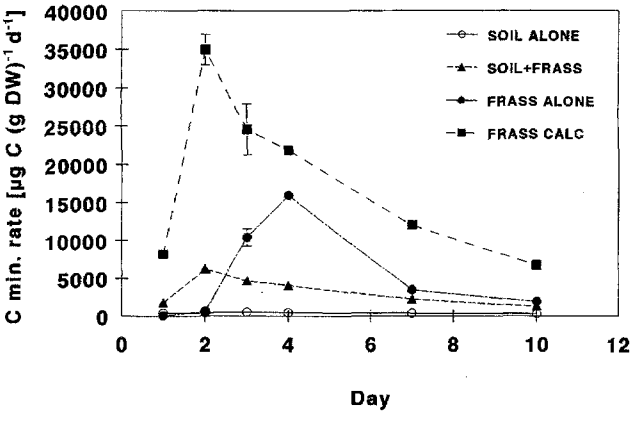
Carbon mineralization

Evolution of CO_2 peaked in the first 5 days of the experiment in the frass and soil + frass samples and declined in a roughly exponential fashion thereafter (Figs. 1 and 2). The soil samples generally had lower rates of CO_2 evolution than the frass or soil + frass samples for the first 30 days of the experiment, and the rates declined slightly during the course of the experiment (Fig. 2). The calculated frass C mineralization rate from the soil + frass treatments (expressed per gram of frass, and called "frass calc" in Figs. 1 and 2) were higher than the rates from the frass alone treatments throughout the first 90 days of the experiment (Fig. 2), indicating either that the soil was an important source of organisms and nutrients for the decomposition of the frass, or that the labile C from the frass "primes" the soil microbial community (Alexander 1977) and increases the mineralization rate of soil C. At the end of the experiment (120 days) the differences between treatments were not statistically significant.

In the first 10 days of the incubation, the soil-alone samples lost an average of 2.2% of the initial C in the sample as CO_2, compared to 13% for the soil + frass samples, and 11% for the frass alone samples. After 120 days of incubation, soil-alone samples had lost 15% of their initial C content, compared to 36% for the soil + frass samples, and 20% for the frass alone. If we assume that all of the CO_2 released from the soil + frass samples in excess of that released from the soil-alone samples represented decomposition of the frass (as opposed to soil priming), then the frass component of the soil + frass mixture lost 30% of its C by day 10 and 72% by day 120.

A visible mat of fungal hyphae covered the frass and soil + frass samples after a few days of incubation, and remained until the end of the experiment. No such fungal mat was visible in the soil-alone samples.

Fig. 1 Mean carbon mineralization rate (CO_2 evolution) for the treatment groups during the first 10 days of the experiment. *Frass calc* is the rate in the frass component of the soil + frass treatment (see text for calculation). *Error bars* are SEs



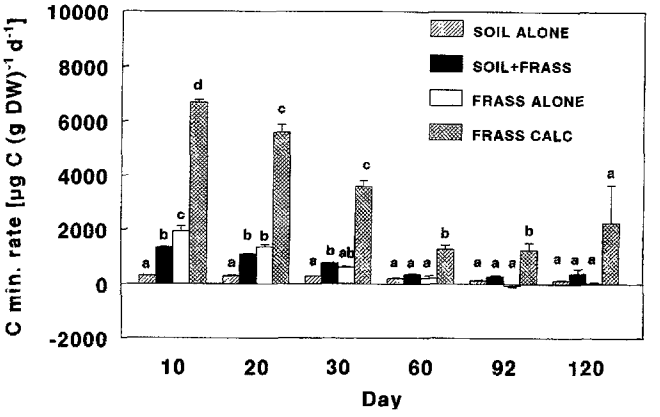


Fig. 2 Mean carbon mineralization rate (CO_2 evolution) for the treatment groups at 10-d intervals during the entire experiment. *Frass calc* is the calculated frass component of the soil + frass treatment (see text for calculation). *Error bars* are SEs. Within a sampling date, *bars* with *common letters* are not significantly different at the $P = 0.05$ level

Nitrogen mineralization

Initial extractions of the samples showed that, compared to the soil alone, the quantities of extractable N (mostly as NH_4^+) were 110-fold greater in the frass samples and 22 fold greater in the soil + frass mixture (Table 1). The N extracted from the frass in both the frass alone and soil + frass samples represented an average of almost 9% of the total N in the frass, compared to 0.2% of the total soil N extracted from the soil-alone samples.

The quantity of N extracted from the frass and soil + frass samples after 10 days of incubation was substantially lower than the time zero samples, suggesting substantial N immobilization by microorgan-

Table 1 Mean extractable NH_4^+ and NO_3^- (µg N/g dry wt) in the initial samples from different treatment groups, with standard deviations in parentheses ($n = 4$ for each treatment). "Frass calculated" represents the frass component of the soil + frass mixture, expressed per gram dry weight of frass

Treatment	Extractable NH_4^+-N	Extractable NO_3^--N
Soil alone	18.6 (1.58)	0.223 (0.00)
Soil + frass	414 (8.42)	7.17 (0.175)
Frass alone	2047 (163)	37.6 (1.70)
Frass calculated	2184 (46.3)	38.2 (0.96)

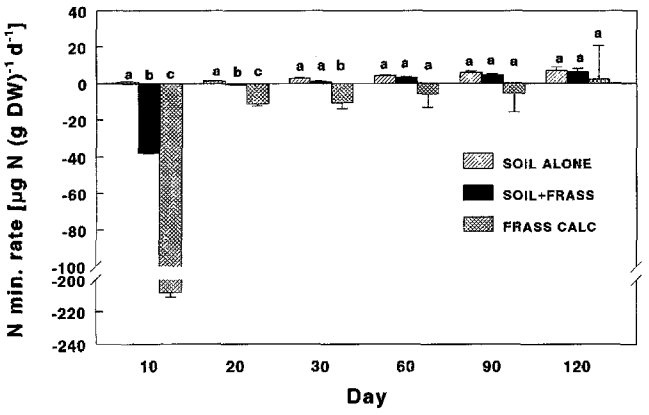


Fig. 3 Mean potential net N mineralization rate for the different treatment groups. *Frass calc* is the calculated frass component of the soil + frass treatment (see text for calculation). *Error bars* are SEs. Within a sampling date, *bars* with *common letters* are not significantly different at the $P = 0.05$ level. *Bars* are plotted at the endpoints of the 10-day or 30-day incubation periods

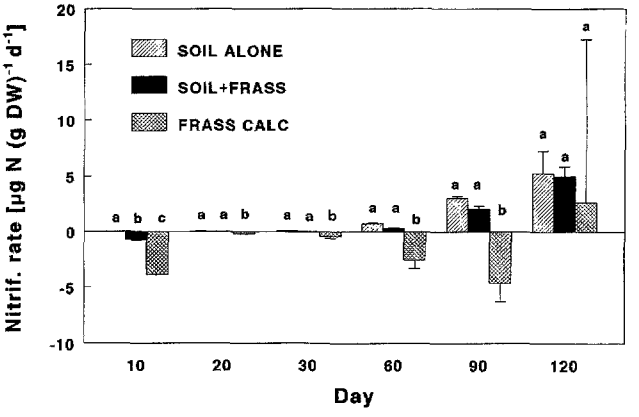


Fig. 4 Mean potential net nitrification rate for the different treatment groups. *Frass calc* is the calculated frass component of the soil + frass treatment (see text for calculation). *Error bars* are SEs. Within a sampling data, *bars* with *common letters* are not significantly different at the $P = 0.05$ level. *Bars* are plotted at the endpoints of the 10-day or 30-day incubation periods

isms in the frass (Fig. 3). In contrast, the soil-alone treatments showed a moderate net N mineralization rate typical of surface forest soils in this area. The rates of potential net N immobilization of the frass in the soil + frass treatment ("frass calc" in Fig. 3) dropped sharply after the first 10-day period and then continued to decrease slowly throughout the remaining 110 days of the experiment, whereas the potential net N mineralization rates in the soil-alone samples increased throughout the experiment. The soil + frass treatment switched from net immobilization to net mineralization between 20 and 30 days, as the net mineralization by the soil began to exceed the net immobilization by the frass component (Fig. 3). The frass-alone samples showed a similar switch from net N immobilization (-64.7 µg m^{-2} day^{-1}) for the 0 to 30-day period to net mineralization (7.4 µg^{-2} day^{-1}) in the 30–90 day period. (The frass-alone data are not shown in Figs. 3 and 4 because the incubation periods do not correspond to those of the other treatments). However, the frass component of the soil + frass samples continued to immobilize N until day 90, although the variance among samples continually increased (Fig. 3, "frass calc").

Potential net nitrification rates showed a similar pattern, with strong immobilization of NO_3^- in the first 10 days by the frass in the soil + frass samples, decreasing to lower levels immediately afterwards (Fig. 4). However, the rate of NO_3^- immobilization increased from day 20 to day 90, after which nitrification began. The soil samples showed no net nitrification in the initial period, but nitrification began by day 20 and increased rapidly thereafter, probably indicating the development of the population of nitrifying bacteria in the samples. By day 120, about 75% of the mineralized N was being nitrified in both the soil and soil + frass treatments.

For both mineralization and nitrification, the "frass calc" mean at 120 days is positive despite the fact that "soil + frass" is less than "soil alone" (Figs. 3 and 4). This is counterintutive but it can occur because the soil-alone and soil + frass data are expressed per gram dry weight of soil or soil + frass, whereas the "frass calc" values are expressed per gram dry weight of frass (Eq. 1). Because this weights individual samples differently, and the samples at day 120 included both positive and negative rates, the sign of the mean can be changed.

Discussion

Although the C : N ratio in gypsy moth frass (20 : 1) is not markedly different from that of surface soils used in this study (23 : 1) or oak foliage (typically 24 : 1), the C in the frass appears to be extremely labile and much of the N readily extractable. In these experiments, the labile C appears to have stimulated microbial (especially fungal) growth to the extent that 94% of the extractable N was immobilized within the first 10 days of the incubation [immobilization rate 208 µg Ng^{-1} dw day^{-1} × 10 day (Fig. 3), divided by 2222 µg Ng^{-1} dw extractable N (Table 1)]. Based on the patterns of microbial activity shown in Fig. 1, most of this immobilization probably occurred in the first 5 days. The immobilized N appears to have been effectively retained in microbial biomass. The net immobilization continued for 30 days of the study, and no significant N mineralization (i.e., significantly different from 0) occurred in the "frass calc" component at any time during the 120-day study. Even though the addition of the frass to the soil samples increased the N content by 67%, the mineralization rate from the soil + frass samples never exceeded the rate from soil-alone samples during the experiment.

The "frass calc" variable includes both the behavior of the frass in the soil + frass mixture and the priming effect of the frass on the soil microbial community, and we cannot definitively separate these responses with the data from this experiment. However, we believe that most of the response from frass addition was from the decomposition of the frass itself, for two reasons:

1. The soil + frass samples mineralized carbon early in the experiment at a rate as much as 14 times that of the soil-alone samples; this is extremely large for a priming effect (e.g., Alexander 1977).

2. Because our soil-alone treatments mineralized N, one would expect that enhanced decomposition of the soil C in the soil + frass treatment would be accompanied by enhanced mineralization of N, yet these samples immobilized N strongly. If soil priming does occur to some extent, we consider it to be part of the response of the soil to frass deposition.

We cannot be absolutely sure that the decrease in extractable N over time is solely a result of microbial immobilization; denitrification and NH_3 volatilization could also have occurred. However, a rough calculation suggests that growth of microbial biomass would have been sufficient to account for the decrease in N. For example, in the soil + frass samples, 29.8 mg C per gram of sample were respired during the first 10 days of the experiment. Assuming a low ratio of biomass production : respiration of 0.2, 6.0 mg microbial biomass C would have been produced per gram of sample. The C : N ratio in fungal and bacterial biomass varies from about 3 : 1 to 15 : 1 (Paul and Clark 1989). Even with a ratio as high as 15 : 1, the N required to produce the new microbial biomass in the soil + frass samples would be 0.4 mg N/g, which is sufficient to account for the apparent immobilization of N during the first 10 days of the experiment (0.38 mg/g). This calculation, plus the observed fungal growth, suggests strongly that microbial immobilization was responsible for most of the decrease in extractable N.

The behavior of a soil + frass mixture will depend on the ratio of soil to frass. We arbitrarily chose a ratio of 4.5 to 1, but in nature the ratio depends on the amount of frass deposition and the depth of soil considered, and thus will be extremely variable. It is therefore difficult to generalize from our experiment to the behavior of soils in the field. Instead, we have compared the soil and soil + frass treatments to illustrate the behavior of the frass component in a soil + frass mixture, and we can use this to infer the fate of frass generated in forests. Our assay was done under temperature and moisture conditions very favorable for microbial growth, which should enhance the rate at which C is respired compared to field conditions. Nonetheless, the available C was sufficient to prevent significant N mineralization by the frass in the soil + frass samples throughout the 120-day experiment. The immobilization would be expected to last at least that long at the slower microbial growth rates characteristic of the forest floor. Since gypsy moth defoliations occur in June and July, this would probably be sufficient to keep the N in frass from leaching during the remainder of the growing season in the north-eastern United States. After leaf drop in the fall, a new supply of labile C from litterfall may result in continued immobilization of the N.

Microbial immobilization is one of several N retention processes that could minimize N losses after defoliation events. Most of the extractable N in the frass was in the form of NH_4^+ (Table 1), so retention on soil exchange sites would be likely, and nitrification would be required to produce significant quantities of the more mobile NO_3^- form. In addition, Lovett and Tobiessen (1993) demonstrated that N deficient oak trees have the capacity for strong uptake of available NH_4^+ even when the trees are defoliated. If tree uptake recaptures the mobilized N, either during the season of the defoliation or after a delay imposed by microbial immobilization and remineralization, N loss from the ecosystem might be avoided altogether. In the long term, the passage of foliar C through an insect gut may alter the quality of the C such that it would result in less incorporation of N in recalcitrant soil organic matter than might be the case for intact oak leaves. In the shorter term, however, microbial immobilization and vigorous tree uptake provide efficient N conservation mechanisms in defoliated forests.

There are few studies on the loss of N in drainage water after insect defoliation. No increased N loss was noted at the Hubbard Brook Experimental Forest in New Hampshire after significant defoliation in 1968 and 1969 (Bormann and Likens 1979). However, Swank et al. (1981) observed increases in stream N export after partial defoliation at the Coweeta forest in North Carolina. The losses began in the same growing season as the defoliation and continued during the next spring and summer. Even though stream concentrations of NO_3^- increased by a roughly factor of ten after this defoliation, the absolute amount of N lost was only about 0.25 Kg N ha^{-1} y^{-1} (Swank et al. 1981). If we assume that the N content of the foliage in that forest was 93 kg N/ha (based on data from another forest at Coweeta reported by Johnson and Lindberg 1992), and that the 33% defoliation (Swank 1988) returned 25% of the canopy N (23 kg N/ha) to the forest floor as frass, the loss rate in streamwater suggests that about 99% of the N in frass was retained by the ecosystem.

Two additional points are worth noting. First, frass is not the only form of N return to the forest floor during a defoliation event. Green leaf fragments and dead insects are also deposited in substantial quantities on the forest floor (Schowalter et al. 1986; Grace 1986), but the N mineralization potential of these components of litterfall is unknown. Nitrogen return in throughfall can also be increased during defoliations due to the damage to the leaves (Stachurski and Zimka 1984; Hollinger 1986; Haines et al. 1991; Seastedt and

Crossley 1984). Second, N in solution may not be the only, or even the principal, means of N loss from defoliated ecosystems. The increased soil moisture resulting from reduced transpiration after a defoliation event may increase the rate of denitrification, and there may also be direct NH_3 volatilization from frass. Either of these processes could contribute significantly to total N losses.

Defoliation clearly represents a major perturbation to the N cycle of a forest. The results of this study suggest that frass stimulates microbial growth, which can effectively conserve the large pulse of N associated with frass deposition during a defoliation. Further research should seek to elucidate the factors which control N loss from forests after defoliation events.

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