Insect Defoliation and Nitrogen Cycling in Forests

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Outbreaks of defoliating insects can have dramatic effects on forest ecosystems. Studies have shown that defoliation can decrease transpiration and tree growth and increase tree mortality, light penetration to the forest floor, and water drainage (Stephens et al. 1972, Campbell and Sloan 1977, Houston 1981). The allocation of carbon to various parts of the tree may be altered, production of defensive compounds in foliage may increase (Schultz and Baldwin 1982), and seed production may decline for many years after defoliation (McConnell 1988, Gottschalk 1990). Shifts in tree species composition (Doane and McManus 1981, Glitzenstein et al. 1990) and changes in the population size of insectivorous birds and other wildlife may also occur (Holmes et al. 1986, USDA Forest Service 1994).

Several studies of insect outbreaks have also indicated an increased loss of nitrogen (N) from forest ecosystems in drainage water following defoliation, suggesting an increase in soil-available nitrogen that is subject to leaching (Swank et al. 1981, McDonald et al. 1992, Webb et al. 1995, Eshleman et al. 1998, Reynolds et al. 2000). Large losses of nitrogen via leaching would reduce long-term forest production in N-limited ecosystems. In addition, the export of nitrate (NO_3^-) to stream water can acidify downstream waters (Webb et al. 1995) and contribute to eutrophication of coastal waters and estuaries (Fisher and Oppenheimer 1991).

At first glance, the view held by many investigators that forest ecosystems leak N in large quantities after defoliation fits the general notion of nitrogen behavior in disturbed ecosystems. Significant nitrogen losses have been observed in response to disturbances such as intensive harvesting (Likens et al. 1970), fire (Bayley and Schindler 1991), and severe windstorms (Schaefer et al. 1996). However, defoliation differs qualitatively from these other disturbances in three ways. First, most of the trees usually remain alive with their woody structure intact after defoliation by insects. (Exceptions are the high mortality rates caused by repeated severe defoliations of hardwood trees or by severe defoliation of conifers.) Second, physical disturbance of the soil is minimal and significant erosion is therefore unlikely to occur. And third, if the trees are

LABORATORY, PLOT, AND WATERSHED STUDIES INDICATE THAT MOST OF THE NITROGEN RELEASED FROM FOREST FOLIAGE AS A RESULT OF DEFOLIATION BY INSECTS IS REDISTRIBUTED WITHIN THE ECOSYSTEM, WHEREAS ONLY A SMALL FRACTION OF NITROGEN IS LOST BY LEACHING

not killed, the time for substantial canopy recovery is often measured in weeks rather than years.

In this article we examine the mechanisms and magnitudes of N-cycle perturbations by defoliation, drawing heavily on the considerable body of research on the gypsy moth (*Lymantria dispar* L.), an introduced lepidopteran that has been the major defoliator of hardwood forests in the northeastern United States during the last 5 or 6 decades (Doane and McManus 1981). We attempt to establish a more coherent view of the likely consequences of defoliation for N cycling, and we make the case that, contrary to the commonly held view, the response of forest ecosystems to defoliation is primarily one of redistribution, rather than loss, of nitrogen.

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Perturbations of the nitrogen cycle

The most direct and obvious consequence of the defoliation of forests is a change in the fate of leaf-derived (foliar) nitrogen. Consider, for example, the upland mixed-oak forests at our research site in southeastern New York State, which contain about 85 kilograms of N per hectare (ha) in foliage during the growing season. (This is typical of deciduous forests in eastern North America [Johnson and Lindberg 1992].) The fate of that nitrogen is shown in Figure 1. In a normal year, small amounts of nitrogen are lost from the canopy as a result of throughfall (precipitation passing through the canopy), insect herbivory, and premature leaf fall during the growing season, but trees resorb the bulk of nitrogen before leaf abscission in the autumn. Resorption and storage of N in plant tissues ensures the availability of N to support growth of new foliage the following spring and creates a relatively tight internal N cycle in trees.

If the forest is defoliated, however, much of the foliar N is diverted to insect feces (frass), green leaf fall, and insect biomass (Figure 1; Grace 1986, Hollinger 1986, Risley and Crossley 1993). Throughfall N also may increase (Stachurski and Zimka 1984, Hollinger 1986, Schowalter 1999). After a summer defoliation, some autumn litterfall and resorption of N from unconsumed leaves or from new leaves flushed after defoliation can still occur. (The N in reflushed leaves may represent an additional subsidy of N to the foliage from the tree's reserves, rather than part of the initial pool of canopy N, as implied by Figure 1.) The diversion of canopy N to green litterfall, insect biomass, frass, and throughfall comes primarily at the expense of resorption (Figure 1; May and Killingbeck 1995). This breaks the tight internal N cycle of the tree and, together with the allocation of stored N to reflushed foliage, will deplete the tree's N reserves.
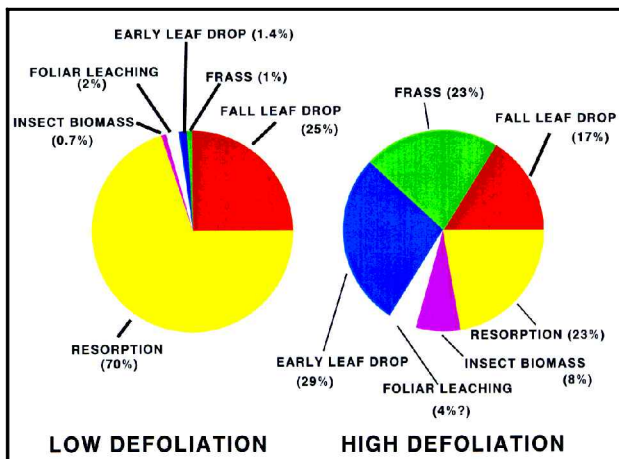

Figure 1. Fate of nitrogen in foliage in years of high and low defoliation in an oak forest in the eastern United States. Data for the low-defoliation case are from upland mixed-oak forests of the Institute of Ecosystem Studies in Millbrook, New York. Data for the high-defoliation case are recalculated from a study of oak forests in Pennsylvania by Grace (1986).

From the point of view of N availability, the key question is, what is the fate of the foliar N consumed by insects and deposited to the forest floor as frass, greenfall, and insect biomass? If trees can readily take up this N, the nutritional consequences of defoliation may not be too severe, although the energetic consequences of having to produce new foliage could still be substantial. Our research on oak saplings suggests that severe defoliation does not diminish a tree's ability to take up N from the soil to support compensatory photosynthesis and production of new foliage (Lovett and Tobiessen 1993). However, if N is lost from the system or otherwise becomes unavailable, the trees could suffer a severe N shortage during recovery. Low N availability has been shown to limit the ability of trees to tolerate or compensate for defoliation damage (Waring et al. 1992, Wickman et al. 1992, Lovett and Tobiessen 1993). The responses are complex, however, because low N supply can also slow the population growth of defoliating insects (Mason et al. 1992) and enhance the induction of a tree's chemical defenses against insects (Hunter and Schultz 1995).

One possible mechanism of ecosystem N loss during defoliation is gaseous N loss from the insect itself. This mechanism seems especially plausible in lepidopterans, many of which use an extremely alkaline gut pH to digest their food. The midgut of a gypsy moth caterpillar has pH 11–12, one of the highest pH levels known in biological systems (Schultz and Lechowicz 1986). Adding plant N to such an alkaline environment is likely to volatilize ammonia (NH_3) vapor, which could escape from the insect's digestive tract. However, in a laboratory experiment, we measured volatilization of NH_3 from gypsy moth caterpillars feeding on oak leaves and found that less than 0.1% of the N consumed was volatilized (Figure 2).

The reason for this apparently tight N retention by the gypsy moth became clear during our research. Although the midgut of the moth is highly alkaline, the frass pellet that emerges from the hindgut is moderately acidic (pH approximately 4 to 4.5; Lovett et al. 1998). Gypsy moths accomplish this remarkable feat of gut alkalization and reacidification through a powerful ion pumping system (Dow 1984). Acidification of the hindgut presumably recaptures any NH_3 vapor generated in the midgut, making the insect relatively leakproof with regard to gaseous N emissions.

This does not mean that the insect efficiently assimilates most of the N it consumes. In our laboratory experiments, approximately 84% of the N consumed by gypsy moth larvae was egested in frass (Figure 2). The amounts of N egested and volatilized indicate that the larvae assimilated only about 16% of the N they ingested (Figure 2), a remarkably low N utilization efficiency compared with other insects (Montgomery 1982). Although over their entire life cycle gypsy moths would very likely use N more efficiently, late-instar caterpillars such as those used in our experiment are known to have low efficiency of N use (Montgomery 1982). These late-instar caterpillars are very important for N cycling because they are responsible for most of the canopy defoliation
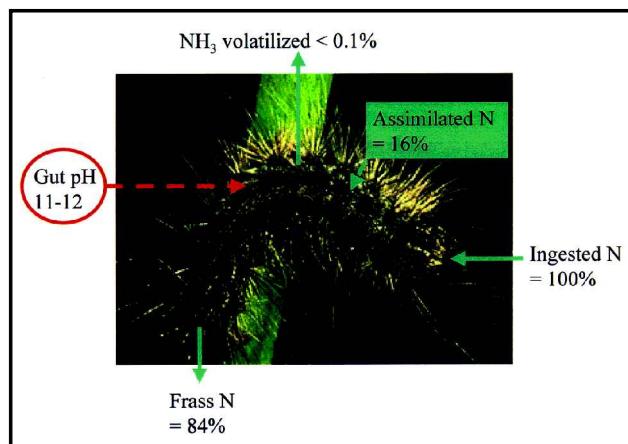
Figure 2. Fate of foliar nitrogen (N) consumed by gypsy moths feeding on oak leaves. Calculated from foliar consumption, frass production, and ammonia (NH_3) volatilization data in the experiment described by Lovett et al. (1998).

(Leonard 1981). In fact, in a real defoliation the insects use the available foliar N even less efficiently because their sloppy eating habits allow a substantial amount of green leaf material to fall to the ground unconsumed (Figure 1).

Chemistry and fate of frass pellets

Our scatological research team has investigated the chemistry and fate of gypsy moth frass pellets. We found that the concentration of N in frass from gypsy moth larvae feeding on oak foliage is about 2.4% (dry mass basis) and the ratio of carbon (C) to nitrogen is about 20, similar to levels in green oak foliage but more enriched in N than is oak litter (Lovett and Ruesink 1995). About 9% of the N in frass is chemically extractable as inorganic forms (NH_4^+ and NO_3^-). The other 91% is presumably in organic forms such as uric acid. The carbon in gypsy moth frass appears to be highly labile and readily consumed by soil microbes, because adding frass to soil in laboratory experiments produces a rapid increase in microbial respiration that can last for several months (Figure 3a; Lovett and Ruesink 1995). The labile carbon fuels rapid microbial growth and results in a significant immobilization of N in microbial tissues, thereby reducing the potential for N mineralization (conversion of organic nitrogen to bioavailable forms of inorganic nitrogen) (Figure 3b).

There are few other studies of the immobilization of N in insect frass with which to compare our findings. Frass additions had no effect on availability of NO_3^- or phosphate (PO_4^{3-}) in the soil in small experimental enclosures in a forest in North Carolina (Reynolds and Hunter 2001). However, Lewis (1998) showed that the frass of elm spanworm (*Ennomos subsignarius* Hubner) larvae immobilized inorganic N when incubated in stream water. Other types of invertebrate excreta may also stimulate microbial N immobilization. Grier and Vogt (1990) showed that aphid honeydew (a carbohydrate-rich secretion produced by aphids during phloem feeding) reduced N mineralization rates in an alder forest in

western Washington. They concluded that the labile carbon in the honeydew stimulated N immobilization by microbes. Similarly, feces from herbivorous snails were shown to reduce N mineralization in a desert ecosystem (Zaady et al. 1996). When water was added to the soil, there was an immediate flush of extractable N from the snail feces, followed by a period of N immobilization. A similar pattern of release and immobilization may be occurring in gypsy moth frass.

Our results indicate that lepidopteran frass, at least for the first few months after defoliation, is a strongly N-immobilizing substrate rather than a N-mineralizing one. Because gypsy moth defoliations occur in early summer (June and July), the months immediately following defoliation are critical to a tree's ability to counteract some of the damage by increasing photosynthetic rates in any remaining leaves (termed *compensatory photosynthesis;* Hodgkinson 1974, Heichel and Turner 1983), flushing new foliage, and replenishing reserves of N. However, all of these recovery responses require available N. For example, low N availability inhibits the compensatory photosynthetic response of oak seedlings after defoliation (Lovett and Tobiessen 1993). Immobilization of frass N in microbial biomass during this critical response period probably hinders a tree's recovery.
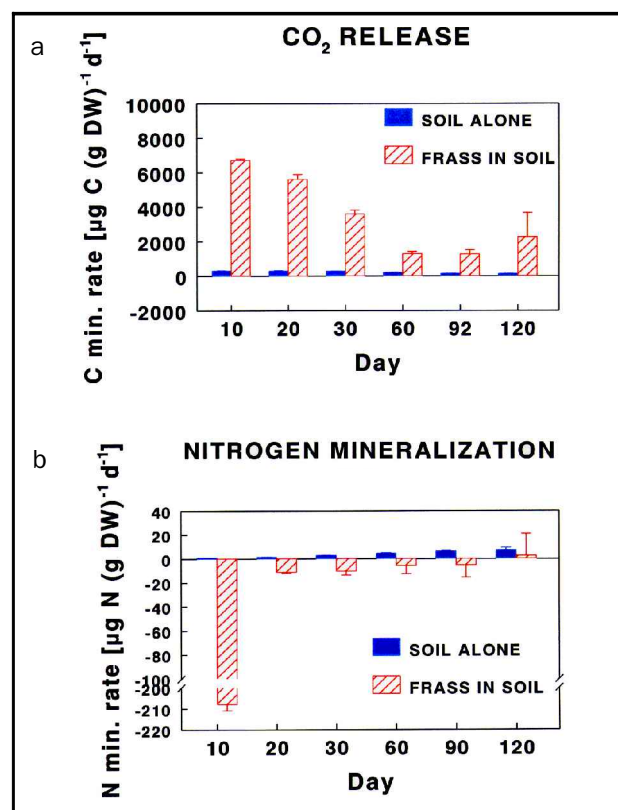
Figure 3. Rates of (a) carbon dioxide (CO_2) release and (b) nitrogen (N) mineralization from laboratory incubations of soil alone and from the frass component of a frass-soil mixture. Negative N mineralization rates indicate immobilization of inorganic N. Data are from Lovett and Ruesink (1995).

What is the fate of this immobilized N over the longer term? We addressed this question in a field study of small plots to which we added frass and oak litter labeled with the stable isotope ^{15}N. By using a small amount of ^{15}N as a tracer, we were able to examine the fate of N in the soil without substantially altering the N cycle. We labeled the leaves with ^{15}N by infusing an oak tree with a solution containing ^{15}N during the period in the spring when the leaves were expanding. We fed some of the green leaves to gypsy moths in captivity, which produced isotopically labeled frass, and collected the remaining leaves during normal autumnal litterfall, producing labeled litter. We added the labeled frass and litter to small trenched plots in a forest in which we planted an oak seedling to act as a bioassay of N availability to plants. We sampled the plots repeatedly over 2 years to determine the fate of the applied ^{15}N (Christenson et al. forthcoming) and measured the distribution of ^{15}N in soil, microbial, and plant pools and its loss via leaching.

Not all of the applied ^{15}N was recovered, despite our intensive sampling of these plots. Recovery averaged 81% for plots that received leaf litter and only 40% for plots that received frass, raising the possibility of additional ecosystem losses of N that we did not measure, such as organic N leaching or gaseous N loss. Ammonia volatilization is unlikely because the pH of the soils was acidic. Denitrification is unlikely because the soils were well drained, although it may have been occurring in the frass pellets themselves. However, gaseous N oxides could have been produced through other processes, such as nitric oxide production associated with nitrification (Firestone and Davidson 1989).

The fate of the recovered ^{15}N was markedly different in the litter treatment plots compared with the frass plots (Christenson et al. forthcoming). In the litter plots, most of the recovered ^{15}N remained in the undecomposed litter; only a small amount was mobilized into the soil (Figure 4). In contrast, the frass dissolved quickly and moved down into the soil, producing a pulse of ^{15}N that found its way into all measured soil and plant pools of N. The concentration of ^{15}N in all measured pools was greater in the frass treatment than in the litter treatment plots. More than 99% of the ^{15}N recovered in the frass treatment plots was in the soil, and only about 1% of that soil ^{15}N was in inorganic, microbial, or mineralizable (as measured in a 10-day laboratory incubation) N pools (Christenson et al. forthcoming). The remainder was in a less available fraction of soil organic matter, but its chemical form and mechanism of incorporation into the soil organic matter are not known. The mechanisms might involve microbial uptake and rerelease of N or abiotic N sorption processes (Berntson and Aber 2000, Johnson et al. 2000). Very little leaching of inorganic N occurred in either the frass or litter treatment plots—less than 0.01% of the applied ^{15}N in both cases. Our data also suggest that the ^{15}N mobilized from litter in the litter treatment plots was less likely to be recovered than the ^{15}N in the frass treatment plots, but the portion that was recovered was more likely to be retained in the surface soils (as opposed to subsoils), and may have been
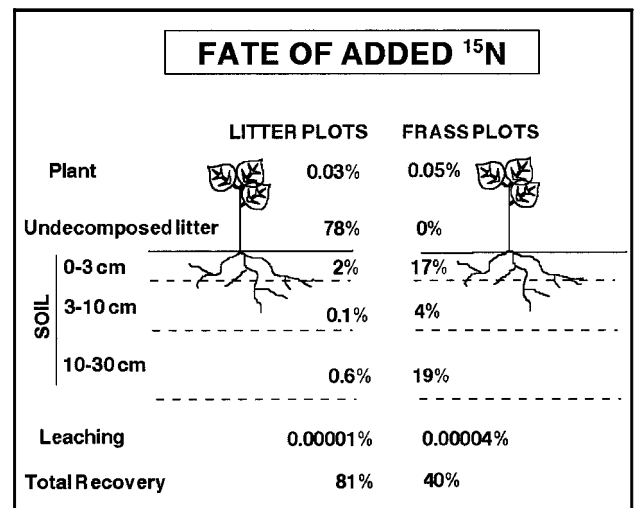

FATE OF ADDED ^{15}N

	LITTER PLOTS	FRASS PLOTS
Plant	0.03%	0.05%
Undecomposed litter	78%	0%
SOIL 0–3 cm	2%	17%
3–10 cm	0.1%	4%
10–30 cm	0.6%	19%
Leaching	0.00001%	0.00004%
Total Recovery	81%	40%

Figure 4. Fate of the ^{15}N tracer added to small trenched plots as either oak litter or gypsy moth frass. Data are percentages of the applied ^{15}N that was recovered in the pools indicated. Data from Christenson et al. (forthcoming).

more available to plants than was frass N (Christenson et al. forthcoming).

The results of this experiment indicate that defoliation interrupts the normal cycling of N through the soil–plant system. Litter N is released slowly during the decomposition process, whereas frass N moves quickly to subsoils, where it is retained in soil organic matter. Both forms of N are tightly conserved within the plant–soil system, but by very different mechanisms and with potentially different consequences for N availability.

Overall, our laboratory and field-plot studies highlight three important conservation mechanisms for N in a forest undergoing defoliation. First, at least in the case of gypsy moth defoliation, the ecosystem loses very little N by volatilization from the insects themselves. Second, N that reaches the ground in frass pellets is subject to rapid immobilization by microbes, and in the longer term by incorporation into soil organic matter. Third, if the trees do not die from the defoliation, their roots are capable of taking up available N in the soil even though their foliage has largely been removed. Although this knowledge has been gained primarily through work with gypsy moths and oak trees, consideration of the mechanisms involved leads us to believe that the same conservation mechanisms will apply in many, and perhaps most, cases of forest defoliation by insects.

Comparison with watershed-scale observations

The tight conservation of N in plants, microbes, and soils and the lack of N leaching in our field-plot experiments seem, at first glance, to be at odds with several studies of watersheds that show increases in stream water export of N from forests after defoliation. On closer examination, however, we find that this apparent contradiction can be resolved if we consider that

the amount of N lost from the watersheds is generally small compared either to atmospheric deposition rates or to the amount of N mobilized by defoliation.

At the Coweeta Hydrologic Laboratory in western North Carolina, increases in NO_3^- in stream water were observed after a partial defoliation by the fall cankerworm (*Alsophila pometaria* [Harris]) in 1969–1970 (Swank et al. 1981) and by a sawfly (*Perisclista* sp.) in 1998 (Reynolds et al. 2000). After the cankerworm outbreak, stream water NO_3^- concentration increased approximately 10-fold, but N export remained very low, peaking at less than 0.5 kg N • ha^{-1} • year^{-1} (yr). Although N deposition to the forest floor was not measured during this defoliation, we have estimated that less than 2% of the insect-generated N deposition was lost via leaching (Lovett and Ruesink 1995).

Hubbard Brook Experimental Forest in New Hampshire, the site of the longest-running ecosystem study in North America, was partially defoliated by the saddled prominent caterpillar (*Heterocampa guttiva* Walker) in 1969–1971. Bormann and Likens (1979) reported that this defoliation had no effect on stream water N export. Lewis (1998) suggested that the lack of a stream water NO_3^- response was attributable to the fact that the maximum impact of the defoliation (about 44% loss of leaf area) occurred over only about 20% of the watershed, while the remainder of the watershed underwent less damage or none at all. Recently, Eshleman and colleagues (1998) suggested that the relatively high N concentrations observed in stream water at Hubbard Brook throughout most of the 1970s could have resulted from this defoliation. However, Goodale (1999) showed that N concentrations in stream water were elevated throughout the White Mountains of New Hampshire during that period, even in watersheds that were unaffected by defoliation. In any event, the data from the Hubbard Brook study do not provide strong or unequivocal evidence of elevated N export after defoliation.

Severe defoliation by the gypsy moth occurred in many forests in Virginia and West Virginia in the early 1990s, with some areas recording more than 90% of the leaf area removed. This defoliation clearly resulted in higher N concentrations in streams in this region, which had nearly undetectable concentrations before defoliation (Webb et al. 1995, Eshleman et al. 1998). Export of NO_3^- from these watersheds after the defoliation was also substantial—on the order of 4 kg N • ha^{-1} • yr^{-1}. This level of NO_3^- export can have a marked impact on acidification and eutrophication of surface waters. Nonetheless, 4 kg N • ha^{-1} • yr^{-1} is only half of the annual N deposition of about 8 kg N • ha^{-1} • yr^{-1} in this area (EPA 1998), so even after this severe defoliation, the watersheds still had a net retention of N. Using the conservative assumptions that the green foliage of these forests contained 60 kg N per ha before defoliation and that 70% of the canopy was removed by the gypsy moth, we estimate that leaching losses accounted for 10% or less of the N removed from the canopy by defoliation.

Lewis (1998) measured the N concentrations in stream water draining defoliated and undefoliated watersheds in north-

ern Pennsylvania. Defoliation by elm spanworms removed roughly 30% of the leaf area of the affected watersheds in 1993, and NO_3^- concentrations in stream water reached their peak in 1994. Lewis (1998) estimated that the defoliation caused N export to increase by 1.0–3.5 kg N • ha^{-1} • yr^{-1} compared with nondefoliation conditions. This N loss was 19%–52% of the estimated N deposition in insect frass plus green litterfall during the defoliation, which is higher than the percentages of N loss in the other watershed studies cited above. Lewis (1998) suggests that the high levels of N availability in watershed soils may have contributed to this difference.

Taken together, these watershed studies suggest that most of the N mobilized as a result of insect defoliations is retained in the ecosystem, which is qualitatively consistent with the laboratory and plot experiments discussed above. However, the fact that in some cases a notable increase in stream N loss was observed after defoliation deserves further attention for two reasons: (1) In some ecosystems, even a small increase in N leaching can have significant consequences for stream and lake acidification, because NO_3^- can leach nutrient cations (such as calcium and magnesium) from the soil and transport soil aluminum and hydrogen ions to surface waters; and (2) our laboratory and plot experiments suggest that N retention processes are so efficient that we might not expect any N to leach from the soil. Thus, it is important to ask what factors might result in N losses from a forest ecosystem after defoliation. This question should be the subject of future research, but on the basis of what we know already, we suggest several factors that could play a role, namely tree mortality, hydrologic bypass, and low N retention in soil.

Tree mortality. If defoliation were sufficiently severe and prolonged to kill a significant percentage of trees, elevated N losses could result. Although our ^{15}N tracer studies indicate that most of the frass N is retained in soil organic matter rather than in vegetation, our sapling studies show that tree roots can compete for that N even after defoliation if the trees are still alive. Death of trees would reduce uptake of the N mobilized from frass, reduce the sink for the large pool of N recycled annually by mineralization from decaying organic matter, and add another large source of N from decaying roots. Such a severe shift in the balance of N sources and sinks in the system could overwhelm soil retention mechanisms and result in leaching losses. Research suggests that high rates of tree mortality occurred in some areas of Virginia after the gypsy moth attack in the early 1990s, which may explain the relatively high N export observed from those watersheds. In the longer term, regeneration of the forest after such a mortality event would produce a strong N sink in the vegetation that would be expected to reduce N losses during forest recovery (Vitousek and Reiners 1975).

Hydrologic bypass. If the forest ecosystem experiences large amounts of precipitation during or immediately after defoliation, the resulting overland runoff could decrease contact of frass N with soil and reduce the prospects for N re-

tention. Similarly, N retention could be low in sandy soils or soils with a large amount of channelized (macropore) flow that inhibits contact between frass N and the soil matrix.

Low N retention capacity in soil. Given our incomplete understanding of the mechanisms by which N retention occurs in soil, it is difficult to speculate about factors that might influence this process. However, two soil characteristics seem obvious enough to suggest here—thin soils and soils with low organic matter content. Both factors would produce a lower pool of the soil organic matter that appears to be the site of most retention of frass N. In addition, sufficiency or saturation of the ecosystem with N, resulting from chronic N deposition, fertilization, or presence of N fixers, may also reduce the soil's ability to retain N. This may have been the case for the Pennsylvania watersheds studied by Lewis (1998), in which high levels of N deposition and export before defoliation suggest N saturation.

Conclusions

Insect defoliation represents a major perturbation to the internal N cycle of the forest, but this perturbation primarily causes a redistribution of N within the ecosystem rather than a large loss of N. During defoliation, nitrogen from the canopy is diverted to green leaf fall, frass, and insect biomass. Consequently, autumnal resorption of N from foliage is reduced, depleting the trees' internal stores of N. Furthermore, the chemical nature of the frass, with its highly labile carbon, appears to give soil microbes a competitive advantage over trees for the N deposited in frass. In one study in an oak forest, N deposited to the forest floor as gypsy moth frass was retained primarily in the soil organic matter pool. Laboratory, plot, and watershed-scale studies all indicate strong retention of N in forest ecosystems after insect defoliation. Even in the worst cases of N loss, forest ecosystems show net retention of N (atmospheric deposition > stream water losses) after defoliation. Although the extent of N loss is not great, defoliation-induced N losses raise important questions about the mechanisms of N retention in forest ecosystems.

Relatively few studies of forest N cycling and defoliation have been done, and mechanistic studies have primarily examined the gypsy moth–oak interaction. Additional studies in different systems would permit more effective comparison and generalization, because defoliators differ in such characteristics as digestive strategy, seasonality of defoliation, and host plant choice, all of which can have important effects on N cycling. Because of the difficulty in simulating defoliation in the field, progress in this area will most likely come from a combination of small-scale plot and laboratory studies and opportunistic studies of real defoliation events at long-term ecosystem research sites.

Among the topics that deserve further research are watershed-scale studies of the mechanisms of N retention and loss after forest defoliations; effects on nutrient cycles of the chronic, low-level herbivory that is nearly always present in forests (Seastedt and Crossley 1984, Schowalter et al. 1986),

as opposed to the severe defoliation events examined in this paper; and the interaction of insect defoliation with other stresses such as climate change and elevated N deposition. For example, accumulation of N in ecosystems could influence insect attack by altering foliar quality (Mattson 1980, Mason et al. 1992, Joseph et al. 1993) and simultaneously altering the system's capacity to retain N (Aber et al. 1989). Understanding the complexity of interactions among these multiple changing factors will require experimental studies and long-term observations coupled with rigorous predictive modeling.

Acknowledgments

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