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Nitrogen cycling in poplar stands defoliated by insects

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Abstract. Large-scale outbreaks of defoliating insects are common in temperate forests. These outbreaks are thought to be responsible for substantial cycling of nitrogen (N), and its loss from the system. Gypsy moth (*Lymantria dispar*) populations within poplar plots were manipulated over 2 years so that the ecosystem-wide consequences of catastrophic defoliation on N cycling could be examined. The quantities of N in leaf litter-fall, ammonia volatilization and soil N pools were estimated across the two seasons. Defoliated leaf biomass was estimated from experimentally derived approximate digestibility factors and added to the mass of senesced leaf to determine total annual leaf production. Throughout the growing season the defoliation treatment peaked at about 40% in year 1 and 100% in year 2. Rapid regrowth after defoliation meant that only 45% of the annual leaf biomass was consumed in the defoliation treatment in year 2, while control plots suffered about 20% consumption each year. In each year, defoliated plots produced 20% more leaf biomass and N than the controls, a phenomenon attributed to compensatory photosynthesis. No substantial losses of N *via* ammonia volatilization, nitrous oxide emission or nitrate leaching were observed. Neither was there any sustained or substantial gain in the soils microbial biomass or inorganic N pools. These observations suggest that the defoliated poplars were able to compete with soil microbes and N loss mechanisms for soil N as it became available, thereby ameliorating the effects of defoliation on soil nitrogen cycling. We conclude from this study that the N mineralized from defoliation residues was conserved in this plantation ecosystem.

Introduction

Insect herbivory can regulate forest productivity, succession, and community structure through its effects on nutrient cycling (Mattson and Addy 1975; Showalter et al. 1986; Ritchie et al. 1998). Phytophagous insect populations can defoliate extensive areas of forest, with a short-term consequence of rapid and substantial transfer of foliage to insect biomass and the forest floor. This is an important feature of many forested landscapes, yet its long-term consequences are not well understood. Nitrogen (N) transformations promoted by defoliation may lead to N loses and potential effects on forest net primary productivity, and nutrient retention, that could be long-term (Schowalter et al. 1986; Ruess et al. 1998). This may also affect

N loads in watersheds that drain the defoliated forests (Swank et al. 1981; Reynolds et al. 2000).

The residues from insect defoliation include frass (insect feces), green-fall (green leaf debris), insect cadavers, and senesced plant tissues. These residues are of high quality (low C:N ratio) and under favorable conditions will mineralize rapidly. Frass is believed to be analogous to other animal manures in its potential to mineralize and volatilize ammonia. Animal manures contain large quantities of ammoniacal-N (i.e., urea and ammonium), of which much is lost to the atmosphere as ammonia if the manure remains on the soil surface for more than a few days (Vallis et al. 1982; Sommer et al. 1991). Lovett and Ruesink (1995) concluded, based on laboratory incubations, that there is sufficient labile C in gypsy moth frass to immobilize most of the mineralizable frass N. However, immobilization may be less likely under field conditions where inorganic N derived from frass can be lost *via* ammonia volatilization, denitrification, and nitrate leaching.

Nitrification, which results in the formation of nitrate from ammonium, is often stimulated by severe forest disturbance (Vitousek et al. 1982). Aside from N loss by fire and biomass export, the process of nitrification is the most critical step in the susceptibility of an ecosystem to lose N. Nitrification promotes the accumulation of soil nitrate and therefore promotes soil N loss by hydrologic and gaseous pathways (Haynes 1986). Nitrification readily occurs in forest soils that are disturbed and incubated (Robertson 1982). However, the high plant demand for soil ammonium in undisturbed forests can result in minimal levels of nitrifier activity (Stark and Firestone 1996). Considerable nitrate leakage from Appalachian forested watersheds has been observed after substantial defoliation by fall cankerworm (*Alsophila pometaria*, Swank et al. 1981), sawflies (*Periclista* sp., Reynolds et al. 2000) and gypsy moth (*Lymantria dispar*, Webb et al. 1995; Eshleman et al. 1998). In each case, the nitrate leakage lagged several weeks behind the defoliation event.

In this study, populations of gypsy moths within poplar plots were manipulated to effect catastrophic defoliation. Measures were then made of the quantity, quality and fate of N contained in the defoliation residues. The following hypotheses were constructed. (1) Defoliation will cause an immediate and substantial loss of N, much of the loss as NH_3 volatilized from frass, but a major portion also from hydrologic loss of soil nitrate-N subsequent to defoliation. (2) Defoliation will reduce both plant transpiration and shade, resulting in wetter and warmer soil which promote mineralization, nitrification, and water and nitrate movement. (3) Defoliation will induce leaves of higher C:N ratio in the subsequent season, a consequence of plant N limitation due to ecosystem N loss.

Materials and methods

Site description and experimental design

Experiments were conducted in four replicate blocks of hybrid poplars (*Populus* × *euroamericana* cv. *Eugeneii*) on the W.K. Kellogg Biological Station's

Long Term Ecological Research (KBS-LTER) site in southwest Michigan, USA. The site is on a Kalamazoo sandy loam soil (Typic Hapludalf) planted to agronomic and forage crops for approximately 100 years before the poplars were planted as one of several LTER treatments in 1989 (Marino and Gross 1998). At the start of the LTER study, soil organic C and soil C:N averaged 1.08% and 10.0, respectively, and available soil P levels were high, about 70 $\mu g\, P\, g^{-1}$ soil (Robertson et al. 1997). At the commencement of the present study the poplar stands were in their eighth year of growth, approximately 10 m in height.

This study compared two treatments within a larger experimental design described by Kosola et al. (2001). Each experimental block was a 40 m × 40 m area in the northeast corner of a 1 ha stand of trees. Poplars were planted in a 1 m×2 m array and kept free of understorey vegetation by herbicide applications each year to facilitate an associated study on poplar root responses to defoliation (Kosola et al. 2001). Prior to 1996, gypsy moths were present in the plots at low but detectable levels, having invaded the area within the last decade. To create densities sufficient to cause substantial defoliation, we introduced large numbers of gypsy moth egg masses into the plots in May of 1996 (year 1) and 1997 (year 2).

Rainfall was measured at a nearby automated weather station, while soil temperatures (0.05 m) were recorded in each treatment plot of one block over much of the study. In year 2, soil moisture (0–0.5 m) was measured manually *in situ* by time domain reflectometry (TDR). TDR probes were inserted at two locations within each plot. Time delay data were converted to volumetric soil moisture by the equation of Hook and Livingston (1996) . Soil temperature and moisture differentials were calculated from the difference between defoliated and control plots.

Litter collection and estimates of leaf defoliation

In each plot, litter-fall was collected in two traps (0.5 × 1.0 m) of 1 mm nylon mesh that were placed between rows and adjacent to trees of average breast height diameter (i.e., 1.4 m). Litter within the traps was pooled across collection dates for each trap in each year. Litter of leaf origin was retained and later separated into frass, green-fall and senesced leaf. Litter-fall samples were air-dried, coarse sieved (50 mm) to remove senesced leaves and elutriated with air to separate the dense frass pellets from the green-fall. Insect cadavers were discarded as they were rarely found in the traps; this has been observed elsewhere (Ohmart et al. 1983; Risley and Crossley 1988). The fractions were dried (60 °C, 48 h), weighed, sub-sampled, ground to a powder, and analyzed for total C and N on a Carlo-Erba CN analyzer.

The mass of insect defoliated leaf is the sum of the consumed leaf and green-fall fractions. Consumed leaf was calculated from the mass of frass once converted to its leaf equivalent from an experimentally derived caterpillar approximate digestibility (AD) factor:

$$\text{Consumed leaf} = \frac{\text{frass}}{1 - \text{AD}}$$

The same calculation was performed to estimate the mass of defoliated leaf N. AD was determined to be 0.45 for biomass and 0.55 for N (Parry 2000). The higher value of AD for leaf N reflects a lower proportional retention in the frass of N over carbon (i.e., biomass). Total leaf biomass and N production for each season were then calculated from the sum of the 'defoliated' and 'senesced' leaf litter fractions.

The chemistry of frass

Fresh gypsy moth frass was collected from fifth instar caterpillars feeding on poplar leaves in four micro-cosms. The fresh frass was pulverized and analyzed for an approximation of its ammoniacal-N fractions (i.e., ammonia, ammonium and urea). These fractions were; ammonia-N volatilized within the microcosm, ammonia-N volatilized while oven dried (60 °C, 72 h), ammonium-N in oven dried frass, and the urea-N in oven dried frass. Ammonia-N volatilized within the microcosm was determined from an acid trap inserted in the closed micro-cosms and the acid trap analyzed as for field ammonia volatilization measures (described below). Ammonia loss from oven drying was calculated from the difference between ammonium-N in fresh and dried frass extracted with 1 M KCl solutions. Urea-N was calculated from the ammonium-N content of urease-treated 1 M KCl extracts from fresh frass (Keeney and Bremner 1967). All measurements of ammonium-N were determined as for soil ammonium. The oven dry sub-samples were also analyzed for pH (1:10, w/v water), pH buffer capacity (Strong et al. 1998), total N and total C.

Gaseous-N sampling and analysis

Ammonia volatilization from the soil surface was measured weekly throughout the growing season (May–September) in both years. Ammonia gas was trapped on dry acidified paper over a 24 h period in duplicate static chambers (0.3 m id). Each static chamber consisted of a collar over which a pail was placed. Collars were inserted (0.05 m) into the soil along the tree row, 0.2 m from a tree approximating the average breast height diameter. Large filter papers (0.24 m id, Whatman #1) were acidified in the laboratory by saturation and rapid evaporation of an oxalic acid (3%, w/v) acetone solution (Fox et al. 1994). The acidified papers were stored in sealed double plastic bags until applied in the field. At the end of the 24 h trapping period each paper was placed in a sealed container and extracted with 100 ml of a 1 M KCl solution. Each solution was filtered ($< 2\,\mu m$) and analyzed for ammonium-N as per soil ammonium analysis.

Soil sampling and analysis

All soil samples, composited from five stations within each plot, were sieved (< 4 mm) to remove gravel prior to sub-sampling. Gravel was discarded and the sieved soil was refrigerated until analyzed. The depth of soil sampled was 0–0.15 m in year 1, and 0–0.05 and 0.05–0.15 m in year 2. Sub-soil at 0.15–0.25 m was

sampled at the start and end of the field season in year 2. Duplicate sub-samples (20 g) from each composite were analyzed for gravimetric moisture content (60 °C, 72 h), ammonium-N and nitrate-N concentrations (1 M KCl extraction, segmented flow autoanalyzer; Alpkem, Wilsonville, OR), and microbial biomass N content (Chloroform Fumigation Incubation, Horwath and Paul 1994). In year 2, the surface soil (0–0.05 m) was further analyzed for nitrogen mineralization potential, relative nitrification potential, and nitrification enzyme activity. Nitrogen mineralization potential is the inorganic-N accumulated upon incubation, whilst the relative nitrification potential is the proportion of the mineralized-N occurring as nitrate-N (Robertson 1982). Both of these parameters were derived from a 21-day aerobic incubation (25 °C) at moisture contents close to field capacity. Nitrification enzyme activity is a measure of the rate of nitrification, of added ammonium, in a fresh soil sample during a 24–30 h soil slurry incubation. The slurries being optimized for water content, ammonium concentration, aeration and pH (Hart et al. 1994) .

Nitrate concentrations were also determined on sub-soil water samples. These samples were collected from the sandy C horizon (~1.0 m), when water was available, at monthly intervals between May 1996 and March 1998. Soil solutions were collected *via* teflon-coated quartz suction samplers (Prenart, Denmark) positioned at the center of each plot. These samplers were installed and sampled prior to treatment initiation, and sampled for several months after leaf senescence in both years. The samplers were attached to an extension tube and installed at the base of an augured hole. Before the sampler was installed, the base of the hole was filled with a silica flour water slurry to ensure good sampler-soil contact. After installation, the hole was repacked with soil to prevent preferential flow. Soil solution was acquired *via* a sealed flask attached to the extension tube and fitted with an evacuation tube connected to a hand pump.

Statistical analysis

The plot was considered to be the experimental unit and litter traps and chambers were sub-samples that were averaged for analysis (Hurlbert 1984). Statistical analyses were performed using GLM and ANOVA procedures in SAS (SAS Institute 1988) and the strength of the relationships between variables was examined by regression analysis (Gram-Schmidt algorithm, Coplot, CoHort Software, Minneapolis, MN).

Results

Site environment

The time-course of annual cumulative growing season precipitation (May–September), soil temperature, and the differentials in soil temperature and soil moisture are displayed in Figure 1(a)–(d). Growing season precipitation was 350 mm in year

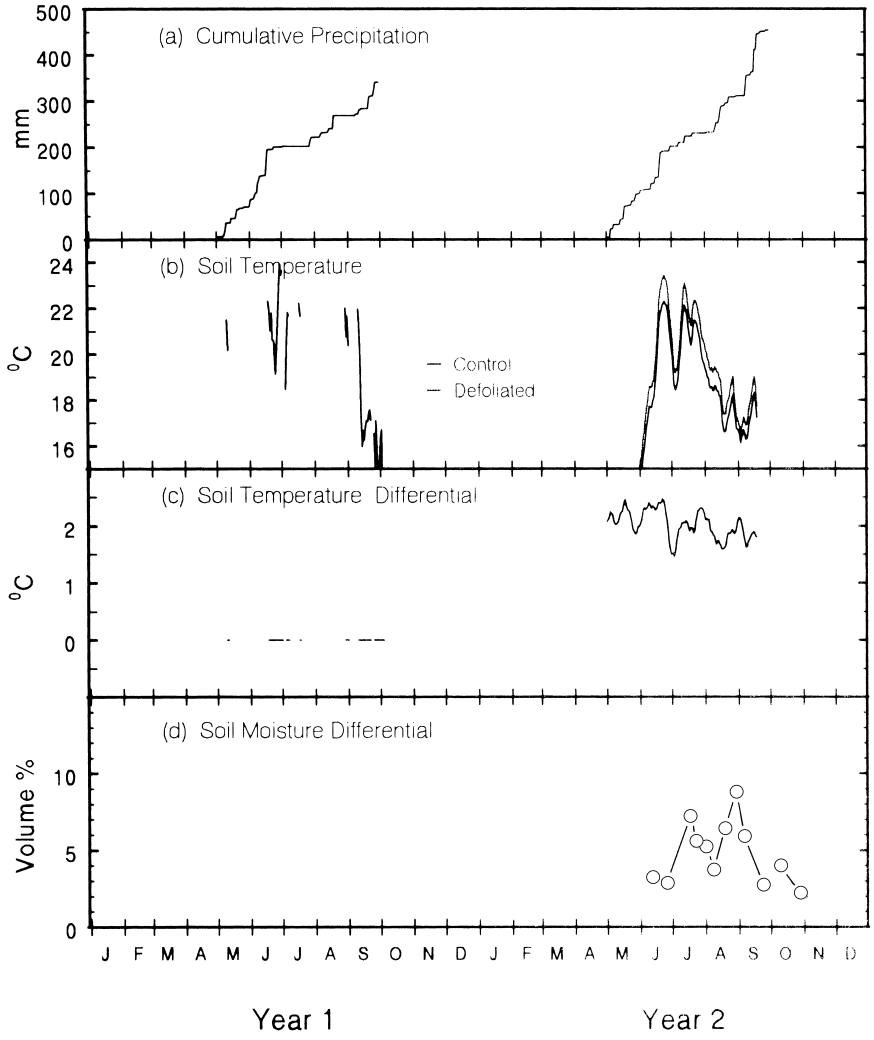

Figure 1. Time-course of environmental parameters; (a) cumulative growing season precipitation, (b) daily mean 0.05 m soil temperature, seven day average, (c) 0.05 m soil temperature differential, and (d) 0–0.5 m soil moisture differential.

1 and 470 mm in year 2 (Figure 1(a)). The year 1 precipitation pattern was characterized by a drought, with no rainfall recorded over a 6 week period in June and July. This placed a severe stress on the poplar stands and induced a substantial (~50%) senescence of poplar foliage by late August.

Daily mean soil temperatures are displayed only where the temperatures rose above 15 °C for the data available (Figure 1(b)). Daily mean soil temperatures for the few days of measurements in year 1 showed no difference between the defo-

Table 1. The approximate partition of ammonia-based nitrogen fractions within mature fresh frass. Total frass nitrogen content was 2.5% of dry weight.

Ammoniacal fraction	Mean ($mg\,N\,kg^{-1}$)	CV (%)	Proportion (% of total N)
AV-Fresh[1]	277	25	1.1
AV-Dry[2]	3164	30.9	12.7
Ammonium[3]	1866	25.4	7.5
Urea[4]	6708	10.3	26.8

[1]Ammonia-N volatilized (AV) within the micro-cosm.
[2]Ammonia-N volatilized (AV) while oven dried.
[3]Ammonium-N in oven dried frass.
[4]Urea-N in oven dried frass.

liated and control plots. In year 2, continuous daily mean soil temperatures were available from May 1 to September 18. Over this period soil temperatures varied from 7 to 25 °C, the defoliated plots being on average 2 °C warmer for the entire duration. Soil moisture data from year 2 showed that significantly higher soil moisture ($P < 0.01$), occurred within the top 0.5 m of soil in the defoliated plots at several times subsequent to the defoliation period (July–September, Figure 1(d)). The defoliated plots were on average 22% (i.e., 4.8% by soil volume) more moist than the controls over this period.

Frass properties

The gypsy moth frass had a total N content of 2.5%, total C content of 50% and a C:N ratio of 20. The frass had a pH of 5.5 and pH buffer capacity of $128\,m\,mol\,H^{+}\,pH\,unit^{-1}\,kg^{-1}$, compared to a site soil pH of 6.5 and soil pH buffer capacity of $3\,m\,mol\,H^{+}\,pH\,unit^{-1}\,kg^{-1}$. The approximate partition of ammonia based N fractions within mature fresh frass is outlined in Table 1. Of the total frass-N, 48% was estimated to be ammoniacal-N with 21% ammonium/ammonia-N and 27% urea-N. About 14% of the frass-N was considered to be susceptible to volatilization (i.e., AV-Fresh + AV-Dry).

Annual leaf-litter dry matter and nitrogen content

The mean annual mass of leaf biomass and N in frass, green-fall, defoliated, and senesced leaf fractions, along with their combined totals are reported in Figure 2. Total leaf biomass ranged from 3155 to $4116\,kg\,ha^{-1}$, equating to N contents of 53 to $61\,kg\,N\,ha^{-1}$, with the defoliated plots yielding about 20% higher in each year. Frass deposition in control plots was similar across years, while frass deposition in defoliated plots was 20% greater in year 2. Interestingly, green-fall in defoliated plots was negligible in year 1 ($< 100\,kg\,ha^{-1}$), but about five times higher in year 2 where it was almost equivalent to frass in both biomass and N content. Defoliated leaf was between two (year 1) and two and a half (year 2) times greater in the defoliated treatment, being greatest in quantity in the second year where it

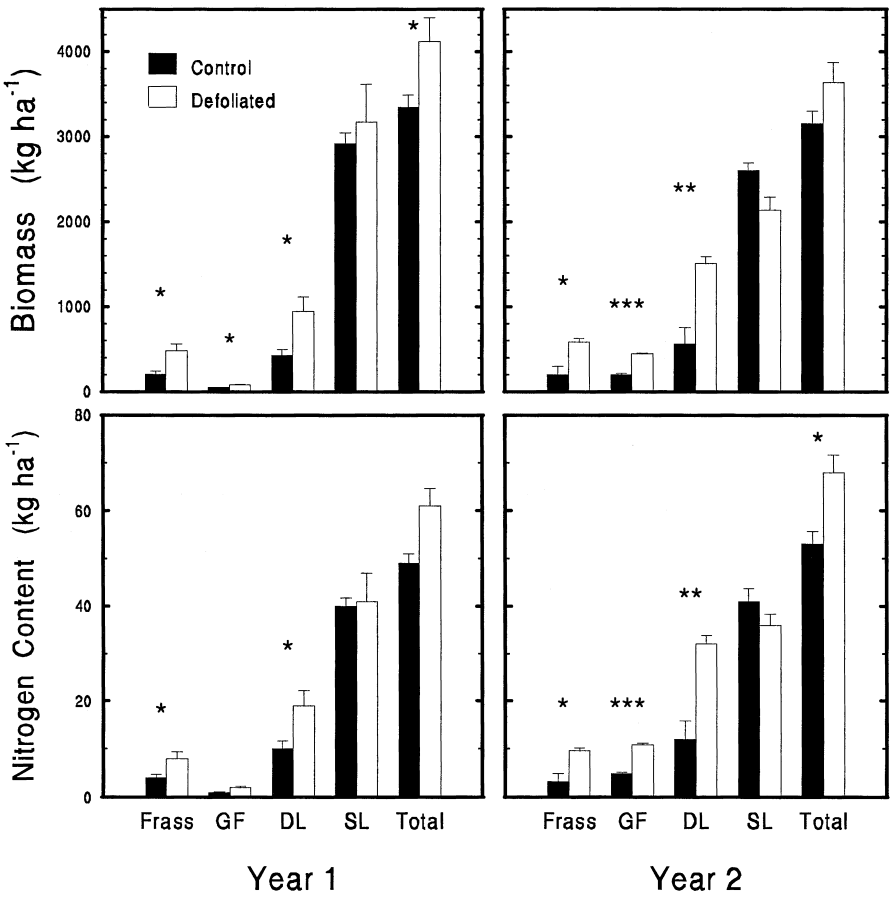

Figure 2. Biomass and nitrogen content of leaf derived litter residues collected inside the plots for both years. GF = green-fall, DL = defoliated leaf, SL = senesced-leaf, and total = DL + SL. Values are mean data from four blocks and error bars are standard errors of the mean. Error bars not shown are smaller than the symbol. $*P \leq 0.05$; $**P \leq 0.01$; $***P \leq 0.001$.

approximated 1503 kg DM ha^{-1} and 25 kg N ha^{-1}. The biomass of the senesced leaf was slightly higher in the defoliated treatment in each year (10–22%), with little difference measured in their N yields. Year 1 senesced leaf biomass was about 30% higher than year 2 regardless of the treatment, yet the N yields across seasons were similar. Senesced leaf in year 1 accumulated at two distinct times. About 50% of the leaf fell in August in response to the summer drought, the remainder upon natural senescence throughout October.

The annual defoliation loss of leaf biomass and N in each plot was calculated from the defoliated-leaf expressed as a percentage of the total annual leaf production. Annual defoliation loss of leaf biomass and N from the defoliated plots were about twice that of the control plots in both years, the loss being significant in

Table 2. Carbon to nitrogen ratios of the green-fall and senesced-leaf litter collected in each year. Values are mean ± standard error; $n = 4$. Control and defoliated values were not significantly different ($P < 0.05$) for either litter fraction, but were significantly higher in year 2 ($P < 0.0001$).

Treatment	Year 1	Year 2
Green-fall		
Control	18.0 ± 0.1	19.2 ± 0.5
Defoliated	17.0 ± 0.6	18.5 ± 0.7
Senesced-leaf		
Control	28.7 ± 0.9	33.0 ± 0.8
Defoliated	26.8 ± 0.7	34.6 ± 0.7

year 2 (biomass $P < 0.05$; N $P < 0.01$). Leaf loss in the defoliation treatment was estimated at 24% of leaf biomass (33% of leaf N) in year 1 and 41% of leaf biomass (42% of leaf N) in year 2.

Carbon to nitrogen ratios of green-fall and senesced leaves were not significantly different between treatments, but were significantly higher ($P < 0.001$) in year 2 (Table 2). While green-fall C:N ratios were up only slightly (~ 1.5 units), senesced leaf ratios were considerably higher (~ 5 units).

Defoliation dynamics

In both years, defoliation residues (frass and green-fall) were deposited on the soil surface by early July, the commencement of the gypsy moth's annual pupation. About 80% of the annual defoliation residue accumulated in the last 2 weeks of June (data not shown). Measurements of canopy light transmission, which is directly related to leaf area index (Buckley et al. 1999) , provided an index for the temporal dynamics of standing leaf mass and defoliation intensity (Figure 3(a)). Significant effects of defoliation on canopy light transmission occurred in both years (Kosola et al. 2001). At the cessation of defoliation activity in year 1 there was little visual difference in poplar foliage between treatments. In year 2, peak defoliation at the end of June eliminated most of the canopy, leaf regrowth was rapid, and canopy densities in the defoliated plots were reduced until August (Kosola et al. 2001) .

Gaseous nitrogen dynamics

Annual cumulative ammonia volatilization was enhanced in the defoliated plots in both years (Figure 3(b)). This effect was most noticeable in year 1, and ranged from 0.53 to 1.04 kg N ha^{-1}. In both years, treatment responses to ammonia volatilization occurred in June at the onset of substantial caterpillar defoliation activity. There was little ammonia volatilization after August in both years. In year 2, chambers used for AV were also sampled for nitrous oxide accumulation at the end of each trapping period; no detectable concentrations of nitrous oxide were ever observed.

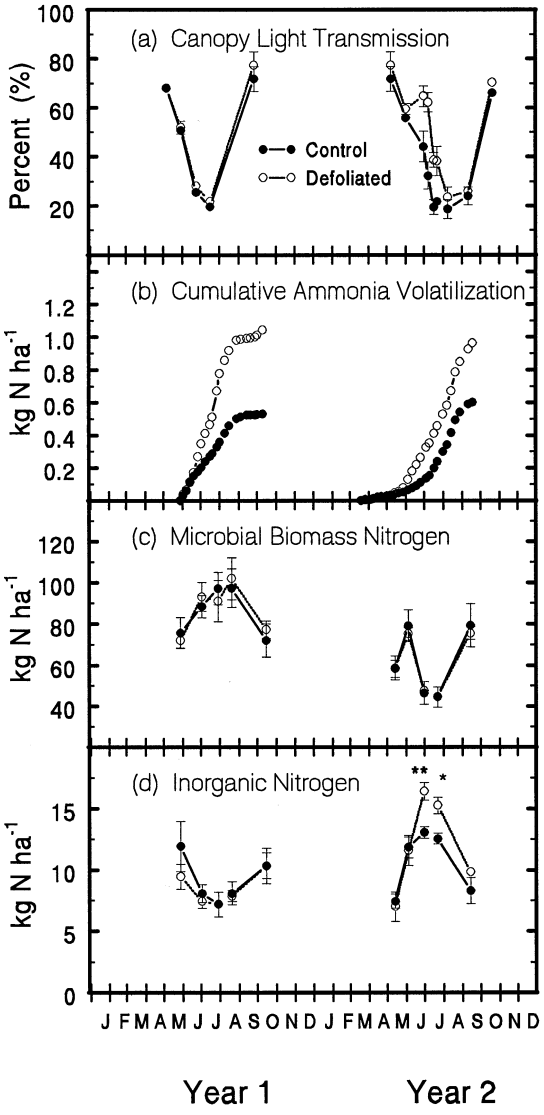

Figure 3. Time-course of defoliation and nitrogen pools; (a) canopy light transmission, (b) annual cumulative ammonia volatilization, and (c) microbial biomass nitrogen and (d) inorganic nitrogen in the top soil (0–0.15 m). Values are mean data from the four blocks, and error bars are standard errors of the mean. $^{*}P \leq 0.05$; $^{**}P \leq 0.01$; $^{***}P \leq 0.001$.

Soil nitrogen dynamics

Soil N dynamics in both years were evaluated from the temporal patterns of microbial biomass N, and inorganic N within the top soil layer of each plot (Figure 3(c) and (d)). While there was little difference in soil microbial biomass N between

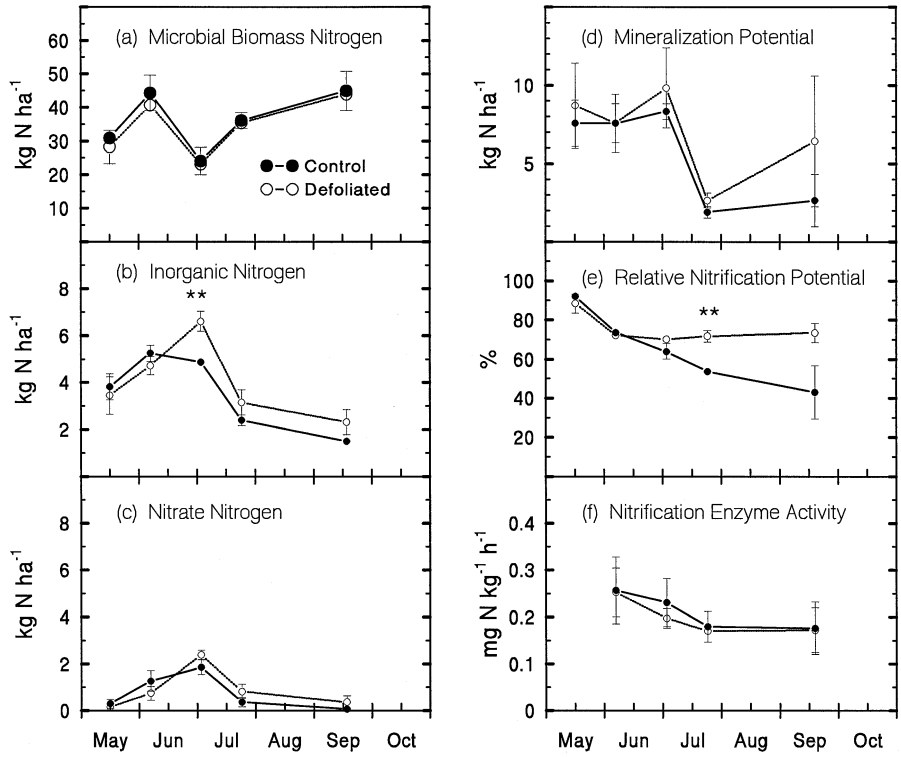

Figure 4. Time-course of soil nitrogen pools and transformations in the year 2 surface soil (0–0.05 m); (a) microbial biomass nitrogen, (b) inorganic nitrogen, (c) nitrate nitrogen, (d) mineralization potential, (e) relative nitrification potential, and (f) nitrification enzyme activity expressed as the rate of nitrate nitrogen formation (f). Values are mean data from the four blocks, and error bars are standard errors of the mean where they exceed the size of the symbol. $*P \leq 0.05$; $**P \leq 0.01$; $***P \leq 0.001$.

the treatments, in both years it was highest for the defoliated treatment at or just after the occurrence of peak defoliation (i.e. July or August, Figure 3(c)). Throughout the summer period (June–August), microbial biomass N was noticeably higher ($\sim 40\,\mathrm{kg\,N\,ha^{-1}}$) in year 1 than year 2. The temporal dynamics of microbial biomass N were different each year, increasing in mid-summer in year 1, and decreasing in mid-summer in year 2. Soil inorganic-N dynamics were quite different from microbial biomass N in each year (Figure 3(d)). In year one, inorganic-N declined mid-season and there was little difference between treatments. In year 2, inorganic-N peaked mid-summer with a significantly ($P < 0.01$) greater quantity (23%) under the defoliated plots at peak defoliation. Measured soil inorganic-N was predominantly ammonium-N in all samples. Only occasionally was there more than $2\,\mathrm{kg\,N\,ha^{-1}}$ ($\sim 10\%$), with a maximum of $6\,\mathrm{kg\,N\,ha^{-1}}$ ($\sim 40\%$), of inorganic-N as nitrate-N in the defoliated plots at peak defoliation.

The soil N pools measured in the surface-soil layer in year 2 were highly correlated with those in the top-soil layer (Figure 4). Approximately one half of the N in the microbial biomass and inorganic-N pools, and one third of the N in the nitrate-N of the top-soil, were located in the surface-soil layer (Figure 4(a)–(c)).

Throughout year 2 N mineralization potentials ranged from 2 to 10 kg N ha^{-1} and were highest at peak defoliation (Figure 4(d)). Errors in the determination of mineralization potential were quite large and there were no significant differences between the treatments ($P < 0.05$). Relative nitrification potentials were very high ($\sim 90\%$) for both treatments early in the year, and remained very high ($> 70\%$) throughout the year for the defoliated plots, while steadily declining to about 40% in the controls (Figure 4(e)). The defoliated plots had significantly ($P < 0.01$) greater relative nitrification potentials than the controls shortly after peak defoliation (ie late July). Nitrification enzyme activity was also highest early in the year, with both treatments diminishing only slightly by the end of summer (Figure 4(f)) . There were no significant differences between treatments for this parameter.

Nitrate-N was not detected in soil solutions below the plots at any time during this study. As for the sub soils sampled in year 2, there were no significant differences between treatments with respect to their inorganic-N or microbial biomass N contents (data not shown). The inorganic-N content of the sub soil was similar to that of the two surface layers (~ 5 kg N ha^{-1}), and largely composed of ammonium-N. The microbial biomass N content of the sub soil expanded considerably over the growing season (7–30 kg N ha^{-1}), to be comparable to that observed in the surface soil layer at the seasons end.

Discussion

The effect of catastrophic defoliation

The impact of the defoliation treatment was much more pronounced in year 2, and resulted in complete defoliation of the poplar stands. This is typical of gypsy moth population dynamics, where after establishing a critical population they can suddenly reach outbreak levels in one season (Weseloh 1985). The modest level of defoliation observed in the controls was not an unusual seasonal scenario. While the catastrophic defoliation achieved in year 2 resulted in about 30% more light transmission into the canopy, this enhanced irradiation was short lived, dropping to 5% within 3 months, at a time just prior to annual senescence. The enhanced irradiation and reduced transpiration of the defoliated plots raised soil temperatures and soil moisture slightly for the duration of the growing season.

In spite of the more favorable environmental conditions for N loss upon defoliation, the N in defoliation residues was highly conserved in these poplar stands. We did not observe any substantial loss of N *via* ammonia volatilization, nitrous oxide efflux, or nitrate leaching. Neither did we observe any sustained or substantial gain in the soil's microbial biomass, or inorganic N pools, after defoliation. This suggests that the poplars, even when defoliated, were able to compete with the soil biota and N

loss mechanisms for soil inorganic-N as it became available. The acidity and buffer capacity of the frass, combined with the reduced soil surface moisture content over the summer months, allowed only modest rates of N release from the defoliation residues, further reducing the potential for N loss from the system. N uptake by defoliated poplars effectively conserved the N that was liberated from mineralized frass and green-fall.

Defoliation residues and leaf production

Due to the variability in caterpillar population and poplar foliage within each plot, the estimation of the mass of defoliation residues is inherently problematic. However, given that the error (%CV) between duplicate litter traps in year 2 were modest (frass 31%, green-fall 18%, senesced leaf 10%), we expect our estimates to be reasonably accurate. To our surprise, the small increase in frass fall in defoliated plots in year 2 compared with year 1 did not reflect the magnitude of change in actual defoliation. Year 2 defoliated plots were observed to have considerably higher green-fall relative to frass, and this suggests that only a slightly higher caterpillar population was required to execute complete defoliation. The slightly higher caterpillar population in year 2 resulted in overcrowding and was more wasteful of leaf than in the previous year.

Leaf emergence was considerably slower in the second year (Kosola et al. 2001), with the resulting annual leaf production being significantly ($P < 0.05$) lower than the first year. This could be attributed to a residual drought effect on N uptake and hence leaf production. However, this could also be confounded with self-thinning effects on annual leaf production, as substantial top dieback was observed in all plots in both years (Kosola et al. 2001). Visual inspection of the plots defoliated in year 2 revealed that defoliation had approximated 100% in all plots. In these plots, over 50% of the total annual leaf production occurred as new growth in the 2 months post-defoliation. In both years the poplars exhibited a tremendous capacity to rebound from defoliation, with the defoliated plots producing about 20% more leaf biomass than the controls. This phenomenon is known as compensatory photosynthesis (Heichel and Turner 1983) and was most pronounced in this study due to the early summer pupation of the gypsy moth's annual life cycle. With defoliation activity ceasing in early July, several months of the growing season remained for the poplars to regain photosynthetic capacity.

Ammonia volatilization

The concentration of ammonium-N in the poplar-derived frass was twice that observed in oak derived frass (Lovett et al. 1998), and probably reflects the higher digestibility of poplar leaves. Although defoliation resulted in significantly higher rates of ammonia volatilization, the mass of volatilized N was surprisingly low ($< 1.2\,\mathrm{kg\,N\,ha^{-1}}$). These masses of volatilized-N were lower than the annual

deposition of ammonium-N at this site, approximately $4\,kg\,N\,ha^{-1}$ (KBS-LTER database), and across this region (Ollinger et al. 1993). The low rates of volatilization are attributed to the inherent acidity and high buffering capacity of the frass, which is known to contain uric acid. The frass pH buffering capacity was 43 times greater than that of the surface soil, therefore any alkalinity generated from the hydrolysis of urea would be readily neutralized by the acidity of the frass, resulting in very low N losses by volatilization.

Soil nitrogen pools

Of the microbial biomass N, inorganic-N and nitrate-N measured in the top soil (0–0.15 m), about two thirds was located in the surface soil layer (0–0.05 m). This is somewhat low for forested soils (Attiwill and Adams 1993), and is attributed to the recent prior agricultural usage of this site. Total soil nitrogen at this site was $\sim 0.11\%$, of which microbial biomass N accounted for 8 and 4% of this in years 1 and 2 respectively. Microbial biomass N is generally observed to be less than 5% of total soil N (Dalal 1998). The excessive amount in year 1 was attributed to the very dry conditions which meant that sampling could only take place after rainfall events, events that may have temporarily caused a flush in the microbial biomass. In these plots there was no N loss *via* surface residue displacement in run off, or nitrate leaching. As the female gypsy moths are flightless and the males die after mating, the N in moth cadavers was considered to be contained within the plots.

Nitrification activity

Nitrification activity was highest (100%) just prior to leaf-out. This suggests that nitrification activity was induced by the spring mineralization flush, just prior to the commencement of poplar N demand. Even though some nitrifiers are well adapted to low ammonium concentrations (Donaldson and Henderson 1989), plants compete strongly with nitrifiers for available ammonium. This was observed in soils from adjacent poplar plots with extensive understory plant communities. Soil collected from these plots during the summer exhibited even lower levels of nitrification activity than the lowest activity measured in the experimental plots. This phenomenon is unlikely to be due to differences in nitrifier strains, as Phillips et al. (2000) showed that the nitrifiers isolated under these poplar stands were largely the same organism found in the neighboring agricultural plots. Eight years of poplar growth had reduced population numbers but not changed the organisms present.

Enhanced nitrification activity in defoliated plots did not lead to noticeable nitrate losses. This was attributed to poplar uptake of soil inorganic-N, even when defoliated. Although saturated rates of ammonium and nitrate uptake by roots were much lower in the defoliated plots, root growth and mortality were not strongly affected by defoliation (Kosola et al. 2001), further evidence that rapid assimilation of soil inorganic-N was possible. Defoliated red oaks have also been observed to assimilate soil inorganic-N (Lovett and Tobiessen 1993).

Other ecosystems

Our results are in strong contrast to studies carried out in the Appalachian mountains where insect outbreaks have been linked to elevated nutrient loads in rivers (Swank et al. 1981; Webb et al. 1995; Eshleman et al. 1998; Reynolds et al. 2000). However, there are substantial differences between these ecosystems. Our plantation consisted of an early successional tree species devoid of an understorey community, and situated on flat topography. Native early successional forests, such as those exemplified by poplar species, are characterized by extensive understorey plant communities and biomass. The lower levels of understorey vegetation in mature Appalachian oak forests, combined with the slow re-foliation of their late successional tree species, predisposes these ecosystems to N loss from catastrophic defoliation. Furthermore, in forests with hilly topography, defoliation residues are susceptible to export into depressions, wetlands, and streams, by the run-off from intense rainfall events. Residues condensed in depressions will promote nitrate contributions to ground water and streams. Clearly, there are aspects of, and complex interactions between, forest community structure, landscape topography, and the frequency and intensity of precipitation, that determine an ecosystems susceptibility to lose N subsequent to a catastrophic defoliation event. Nevertheless, our observations are consistent with Lovett et al. (2002), who recently concluded after considerable investigation of laboratory, plot and watershed insect defoliation events, that the response of forest ecosystems to defoliation is primarily one of redistribution, rather than a loss, of N.

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