

# Impact of a pine lappet (*Dendrolimus pini*) mass outbreak on C and N fluxes to the forest floor and soil microbial properties in a Scots pine forest in Germany

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**Abstract:** Herbivorous insect infestations significantly alter element and nutrient cycling in forests, thus directly and indirectly affecting ecosystem functioning. In this paper, we report on the herbivore-mediated transfer of carbon (C) and nitrogen (N) from the canopy to the forest floor and its influence on soil microbial activity during a pine lappet (*Dendrolimus pini* L.) infestation. Over the course of 6 months, we followed C and N fluxes in bulk deposition, throughfall, and green fall (green needle debris dropped during herbivory) together with solid frass (insect faeces) in an 80-year-old Scots pine (*Pinus sylvestris* L.) forest. Compared with the control, herbivore defoliation significantly doubled throughfall inputs of total and dissolved organic C and N over the study period. Frass plus green-fall C and N fluxes peaked in June–July at 110 kg C·ha<sup>-1</sup> and 2.3 kg N·ha<sup>-1</sup>, respectively. Randomized intervention analysis revealed no significant effects of herbivory on soil microbial properties, except for adenylate energy charge, which showed slightly higher values under herbivory. This study demonstrates the importance of canopy herbivory on overall C and N inputs to forest ecosystems, particularly in altering the timing and quality of the organic material reaching the forest floor and potentially affecting belowground processes.

**Résumé :** Les infestations d'insectes herbivores modifient de façon significative le recyclage des éléments et des nutriments dans les forêts, affectant ainsi directement et indirectement le fonctionnement de l'écosystème. Cet article traite du transfert, résultant de l'action des herbivores, du carbone (C) et de l'azote (N) de la canopée vers la couverture morte et de son influence sur l'activité microbienne dans le sol au cours d'une infestation du bombyx du pin (*Dendrolimus pini* L.). Sur une période de 6 mois, nous avons suivi les flux de C et N dans les dépôts bruts, la précipitation au sol et la chute de litière vivante (débris d'aiguilles vivantes tombées au sol en lien avec l'herbivorisme) ainsi que les excréments d'insectes dans une forêt de pin sylvestre (*Pinus sylvestris* L.) âgée de 80 ans. Contrairement au témoin, la défoliation causée par les herbivores a doublé les apports de N et de C organique totaux et dissous dans la précipitation au sol pendant la période d'étude. Les flux de C et N dans les excréments et la chute de litière verte ont culminé en juin–juillet atteignant 110 kg C·ha<sup>-1</sup> et 2,3 kg N·ha<sup>-1</sup>. L'analyse d'intervention aléatoire n'a révélé aucun effet significatif de l'herbivorisme sur les propriétés microbiennes du sol, à l'exception de la charge énergétique adénylique qui avait une valeur légèrement supérieure à la suite de l'action des herbivores. Cette étude démontre l'importance de l'herbivorisme dans la canopée quant à l'apport global de C et N dans les écosystèmes forestiers, particulièrement en modifiant la qualité de la matière organique qui se retrouve dans la couverture morte et le moment où elle s'y retrouve et en affectant possiblement les processus dans le sol.

[Traduit par la Rédaction]

## Introduction

Phytophagous insects in the canopies of forest ecosystems significantly affect element and nutrient cycling. They directly and indirectly affect ecosystem processes and functions not only in mass outbreak situations but also at endemic (nonoutbreak) density levels (Stadler et al. 2001; Hunter et al. 2003) and are a key factor in regulating canopy processes (Mattson and Addy 1975; Schowalter et al. 1986). As a consequence of their high mobility and reproduction

rates, insects are capable of responding instantaneously to alterations in environmental conditions (Berryman et al. 1987).

Typical defoliation losses due to insect herbivory under endemic conditions are 5%–10% of the annual leaf biomass production in temperate forests (Larsson and Tenow 1980; Ohmart et al. 1983). During outbreak situations, high defoliation intensities of up to 100% are reported, causing remarkable tree growth reductions and mortality rates (Kulman 1971; Lunderstädt 1997; Cedervind and Långström 2003). Exceptionally severe and frequently occurring insect pests are reported for forest ecosystems characterized by low species and structural diversity on one hand and favourable environmental conditions for the development of insects on the other.

Direct effects include modification of the mean element and energy fluxes through the ecosystem (e.g., mean annual throughfall fluxes of carbon (C) or nitrogen (N) in kilograms

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per hectare), thus resulting in changes in resource availability and distribution in the system. A number of field and laboratory studies have analysed the effects of herbivory on nutrient cycling of, for example, inorganic forms of N or phosphorus (P) covering small (laboratory experiments) to large (catchment) spatial scales (Swank et al. 1981; Lovett et al. 2002; Frost and Hunter 2004). Nevertheless, only a few of them addressed the effects on dissolved organic C (DOC) and N (DON) dynamics (Stadler et al. 1998; Reynolds et al. 2000; Stadler and Michalzik 2000); to our knowledge, only Michalzik and Stadler (2005) and Stadler et al. 2006 examined the impact on particulate organic matter (POM) fluxes associated with throughfall.

Because element and nutrient fluxes are conventionally measured after standard filtration (0.45 µm pore size), the exclusion of the POM or unfiltered organic matter fraction (size range 0.45–500 µm) could result in misleading inferences when studying herbivore-mediated element and nutrient fluxes in ecosystems (Michalzik and Stadler 2005). In general, data on the quantity and origin of POM are scarce and, therefore, are seldom considered in terrestrial ecosystem element budgets. One of the rare field studies on POM was conducted by Carlisle et al. (1966) in a sessile oak (*Quercus petraea* (Mattuschka) Liebl.) forest. For particle sizes ≤200 µm, the authors found annual throughfall fluxes of organic C equal to 227 kg·ha<sup>-1</sup>, including a significant carbohydrate fraction of 89 kg·ha<sup>-1</sup>. The readily available C was assumed to originate from microbial and phytophage activity in the canopy (Guggenberger and Zech 1994; Stadler and Müller 2000). Compared with mean DOC throughfall fluxes of 40 and 160 kg C·ha<sup>-1</sup>·year<sup>-1</sup> in temperate forests (Michalzik et al. 2001), the annual extra input by the particulate fraction (>0.45 µm) might result in fluxes between 190 and 70 kg C·ha<sup>-1</sup>.

With regard to the quantity, quality, and timing of the organic matter being transferred from forest canopies to the ground, we suggest that leaf feeders, such as the pine lappet (*Dendrolimus pini* L.), play an important role in forest element cycling, especially during insect mass outbreaks. Apart from enhancing overall organic matter input, the form and timing of inputs are altered. By transforming recalcitrant needle tissue into readily decomposable frass pellets during the vegetation period, they directly enhance the nutrient availability from which subsequent regeneration benefits (Grace 1986; Lunderstädt 1997; Chapman et al. 2006). As yet, it is still under discussion whether these changes in the timing, amount, and quality of available nutrients enhance (Swank et al. 1981; Reynolds et al. 2000; Chapman et al. 2003) or decrease (Ritchie et al. 1998) nutrient cycling in forest ecosystems. As recently pointed out by Stadler et al. (2006), field studies directly quantifying altered inputs of organic matter and elements during insect defoliation and subsequent monitoring of their impact on biotic and abiotic soil processes are difficult to conduct and, hence, scarce.

Some authors suggest that climate change will enhance the frequency of insect pest occurrence, creating intensified stressful conditions with regard to tree performance and defence potential and more favourable growth conditions for pest insects (Mattson and Haack 1987). In this context, a number of extensive insect mass outbreaks were reported following the exceptionally hot and dry pan-European

summer of 2003 (Rouault et al. 2006). The extent to which biologically governed processes and ecosystem interactions will be affected by climatic and environmental alterations is unclear (Hunter 2001), but the current influence of insect herbivory on ecosystem processes has to be determined as basis for assessing future changes.

In the present paper, we report on the direct transfer of C and N compounds from the canopy of a Scots pine (*Pinus silvestris* L.) stand to the forest floor via throughfall, frass (insect faeces), and green fall (green needle debris dropped during herbivory) during a mass infestation of the pine lappet. We also studied the response of the soil microbial biomass C and N and microbial activity as indicated by adenylate energy charge (AEC; Atkinson and Walton 1967). We hoped to link the population ecology of the leaf feeders to the biogeochemistry of the forest ecosystem.

## Materials and methods

### Site description

The study site is located midway between Hamburg and Berlin about 20 km west of the Elbe River in northern Germany. It forms part of the Wendland area and has elevations between 60 and 100 m a.s.l. The climate is classified as subcontinental with rapidly rising temperatures in the spring, dry and warm summers, and large variations in temperature. The mean annual precipitation is approximately 545 mm, and the mean annual temperature is approximately 8.6 °C (German Federal Meteorological Service 1961–1990, Weather Station Lüchow).

The forest site is part of the Prezeller Forst and is planted with Scots pine, which is about 80 years old. The stocking density is 1039 stems·ha<sup>-1</sup>. The understory vegetation consists predominantly of grass and moss as well as volunteer growth. Subsequent to the conclusion of this study, the site was restored to heath land extending the Nemitzer Heide, an existent heath land area, in a northwesterly direction.

The soil type is classified as a podzolic cambisol (Food and Agricultural Organization of the United Nations classification) derived from glacial and aeolian sand deposits and forms an Aeh horizon of 8–10 cm in thickness, followed by a Bw horizon gradually transitioning into the underlying parent material. The forest floor is classified as a moder to raw humus layer of 5–7 cm with C contents of 42% at the infested site and 40% at the control site. Corresponding values for N are 1.3% and 1.2%, respectively, resulting in C/N ratios of 32.3 (infested site) and 33.3 (control site). The pH (H<sub>2</sub>O) of the forest floor at both sites is approximately 4.80 and that measured in KCl 3.05.

### Population ecology of the pine lappet

The pine lappet is a member of the lappet moth family (Lepidoptera: Lasiocampidae) and is one of the most important insect pest species on pines in Eurasia and Germany. In contrast to other moth species that exhibit a polyphagous feeding behaviour, the pine lappet always feeds on coniferous trees.

In Germany, the pine lappet prefers areas with low annual rainfall (500–600 mm) and widely spaced 50- to 100-year-old monocultures of pine growing on dry, warm, sandy sites. Probable reasons for pest occurrence are exceptionally warm

and dry weather conditions during the vegetation period for several years, whereas warm winters with subsequent cold spring and wet summer months lower the risk of lappet outbreaks. Future areas of pine forests at risk in Germany are found in northeastern areas of Lower Saxony, to some extent, but mainly in the state of Brandenburg, where 80% (150 000 ha) of the forested area consists of Scots pine, the result of reforestation actions during the 1940s and 1950s (Majunke and Möller 2003).

### *Life history of the pine lappet*

The flight of the adult moth is normally observed in early to mid-July, in widely spaced timber stands of Scots pine and lasts for 2–5 weeks. The deposition of eggs in form of small loose groups on needles, thin twigs and as well as on the bark follows. In August, the larvae hatch and initially feed only on needle edges and later feed on the whole needle after reaching the third larval stage. In October, the young larvae leave the host tree to overwinter in the forest floor. In early spring when soil temperatures reach 4 or 5 °C, their diapause ends; the larvae crawl up the host trees and begin to feed on old needles and, in part, on May shoots, young bark, and buds as well. During their life cycle, the larvae pass through up to seven larval stages, exhibiting an 11-fold increase in body length from head capsule slippage to pupation and a great increase in the body mass (of approximately 900 times). During the larvae development, the feeding demand initially increases slowly and then accelerates remarkably from the fourth larval stage onwards. The total feeding demand amounts to 15–20 g of needle biomass. This corresponds to 750 needles, of which 90% are consumed by larvae emerging from the diapause. The main fraction of needle biomass is consumed 2–3 weeks before pupation, which starts in June–July in needles and also under the bark for another 4–5 weeks. The life cycle of the pine lappet moth is usually completed in 1 year. However, Majunke et al. 1999 reported that some populations take 2 years to develop, with a second overwintering period.

### **Experimental setup**

Our study covered a period of 6 months. It started on 8 April and ended on 5 October 2005. It focused on the determination of C and N fluxes and their compositions in bulk precipitation (ecosystem input), throughfall, frass, and green fall (internal transfer) and the analysis of soil parameters and soil microbial parameters.

The two experimental sites covered similar areas of 1.65 and 1.96 ha and were both infested with comparable densities of the pine lappet. The pretreatment phase, which provided comparable site conditions, lasted for approximately 3 weeks until the control plot was cleared of moth larvae by helicopter spraying on 30 April 2005, when 75 g·ha<sup>-1</sup> diflubenzuron (trade name Dimilin®) F were applied. Diflubenzuron is a caterpillar-targeting insecticide individually ingested by feeding activity.

Bulk precipitation was collected in two replicates on an open area (heath land) near the forest site using open funnel samplers of 326 cm<sup>2</sup> sampling area. Throughfall was sampled by collectors of the same type and were randomly established in 10 replicates each on the infestation and the control site covering an area of about 40 m × 40 m. Two

throughfall samples each were pooled, resulting in five throughfall samples per study plot and sampling date.

The amount of frass plus green-fall input on the infestation plot was quantified using three nylon nets. The mesh size of the net material was 300 m × 300 µm. Each net was stretched around one pine tree and was individually adjusted to the canopy diameter resulting in differing net areas of 6.5, 6.9, and 7.2 m<sup>2</sup>. Sampling was performed at 6–8 day intervals from May to mid-August (infestation period) and at larger (fortnightly to monthly) intervals until October.

Soil samples from the forest floor (labelled as Oh in the figures and consists of the litter (Ol), fermented (Of), and the humic (Oh) organic layers) and the Aeh horizon were taken with an auger in double replicates. Soil sampling was performed concurrently to bulk and throughfall solution sampling.

### **Chemical analysis**

#### *Solution chemistry*

One aliquot of the bulk or throughfall solutions was 0.45 µm membrane-filtered (cellulose-acetate filters; Sartorius). In this context, the analysis included the determination of DOC and dissolved N (DN) by thermal oxidation (Dimatoc 100, Dimatec, Essen, Germany), and NO<sub>3</sub><sup>-</sup> by ion chromatography (761 Compact IC, Metrohm). From the difference between DN and NO<sub>3</sub>-N, we calculated residual N consisting of NH<sub>4</sub>-N and DON.

In unfiltered aliquots, total organic C and total N (TOC and TN, <500 µm) were also assessed by thermal oxidation (Dimatoc 100, Dimatec, Essen, Germany), where the upper particle size limit of 500 µm was given operationally by the capillary diameter of the TOC/TN-analyser. Particulate organic C (POC) was calculated as difference between TOC and DOC, and particulate organic N (PON) as difference between TN and DN. Element fluxes were calculated from measured water volumes and element concentrations. In addition, the pH (WTW, SenTix 61, glass electrode) and electrical conductivity (EC; WTW, TetraCon 325) were determined.

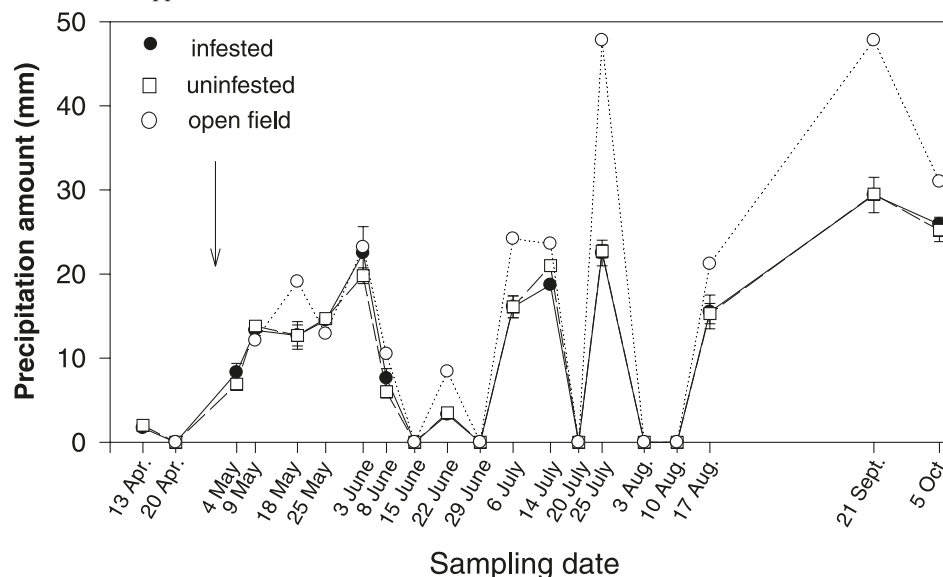
#### *Soil and frass plus green fall material*

In the forest floor and the underlying mineral soil (Aeh) the C and N content (C/N ratio) was measured by elemental analysis (Leco CHN 1000) in double replicates. The solid organic material obtained from the tree nets predominately consisted of frass plus green fall, which was weighed, dried at 45 °C, corrected for dry matter mass, and then analysed for C and N contents. Additionally, C and N were determined in frass material alone (Leco CHN 1000). Insect cadavers were omitted, because they were rarely found in the nets. Input fluxes of C and N by frass plus green fall were calculated from dry matter masses and corresponding C and N contents.

Soil microbial biomass C (C<sub>mic</sub>) and N (N<sub>mic</sub>) was determined by the chloroform fumigation extraction method according to Vance et al. (1987). To characterize the energetic state of the microbial biomass, we additionally determined the individual and total quantities of the adenylates adenosine 5'-triphosphate (ATP), diphosphate (ADP), and monophosphate (AMP) as described in Dyckmans and Raubuch



**Fig. 1.** Amount of throughfall and bulk precipitation at the three experimental sites. Values are means, and error bars are SEs. The arrow indicates when the insecticide was applied.



(1997) and calculated the adenylate ratios to derive the AEC (Atkinson and Walton 1967; Joergensen and Raubuch 2003) using the equation  $AEC = (ATP + 0.5 \times ADP) / (ATP + ADP + AMP)$ . As reported by Atkinson (1977) for in vitro cultures, AEC values of 0.800.95 can be assigned to actively growing cells; values of 0.50–0.75, to dormant cells incapable of biosynthesis; and values <0.50, to dead and dying cells (Brookes et al. 1987). All analyses were performed in double replicates, normally taken at the same sampling intervals as those taken for solution sampling.

### Statistical analysis

To compensate for the fact that only one replicate of each treatment was made and given that the data sets revealed a heterogeneity of variance, we used random intervention analysis (RIA) (Carpenter 1990) to test for statistical differences. RIA is considered a reliable method for determining whether a nonrandom change has occurred in a manipulated ecosystem relative to a control ecosystem after a manipulation. It requires paired time-series data ( $n = 20$ –40 for each treatment group) from both the control and manipulated ecosystems before and after manipulation. In contrast to the before–after–control–impact analysis, it is not affected by non-normality, heterogeneity of variance, or serial autocorrelation (Carpenter et al. 1989). In our study, the pretreatment data covered the period before the insecticide was applied on 30 April.

## Results

### Throughfall fluxes and quality

#### *Throughfall fluxes of total and dissolved C and N compounds*

The quantity and distribution of precipitation at the two experimental sites were quite similar and amounted to comparable water fluxes of about 210 mm over the course of

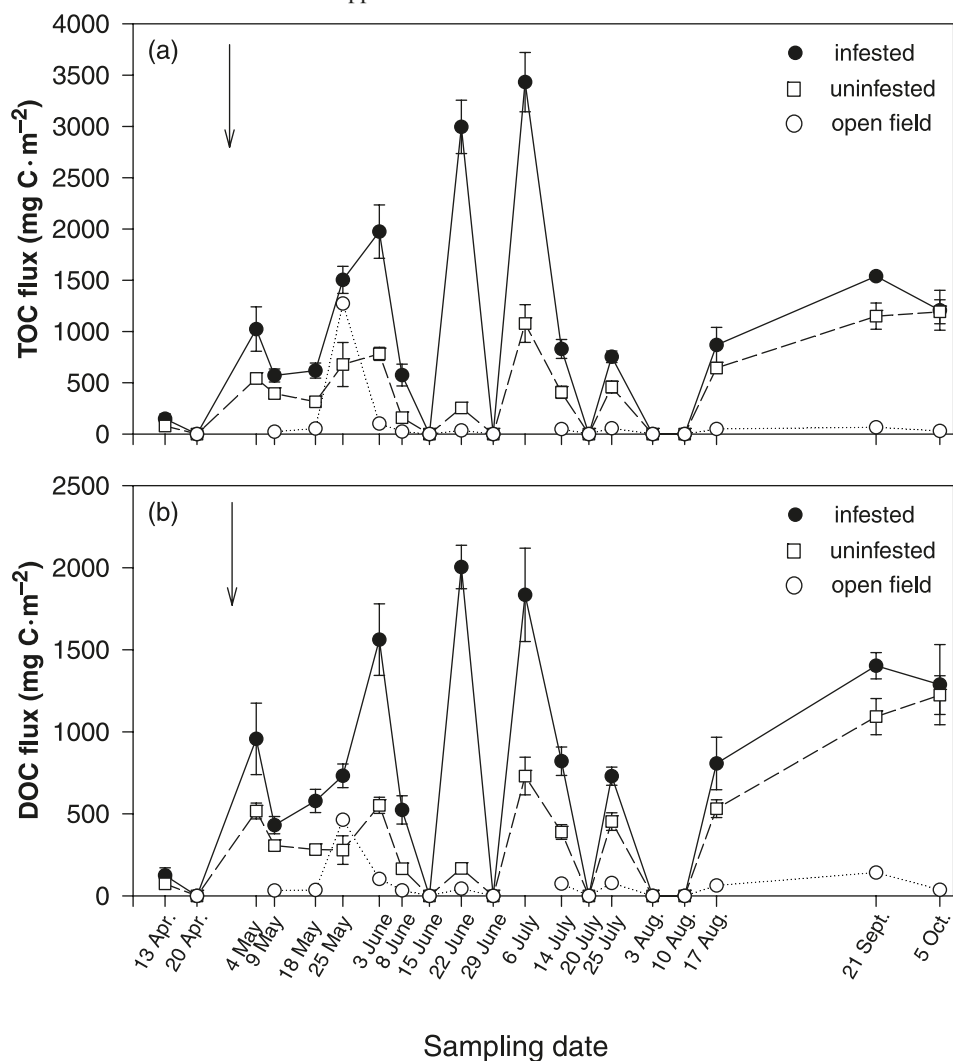
6 months. Bulk precipitation at the open site exhibited 30% higher water fluxes (Fig. 1).

In general, C and N fluxes with throughfall (Figs. 2 and 3) were affected by the frass and feeding activity of the lepidopteran larvae. Based on the life history of the larvae and associated excretory activity (Fig. 4), we discovered a flux pattern under canopy herbivory consisting of four stages: a pretreatment phase in April; initiation of feeding activity during May; increasing and peaking feeding activity and, thus, highest frass plus green-fall production from June to mid-July; and, finally, an abrupt decrease in organic matter input fluxes at the infested site indicating the decrease in larvae abundance and feeding activity (pupation and subsequent metamorphosis to adults).

Consequently, throughfall fluxes of TOC and DOC were governed by the current rainfall and more pronouncedly by the larval abundance and feeding activity. Fluxes in April showed no differences between the infested and the control site; this subsequently changed in May, when DOC and TOC fluxes under herbivory exceeded those of the control by 40%–120%, respectively (Fig. 2). The largest fluxes of C compounds occurred in June and early July, peaking at approximately 2000 mg C·m<sup>-2</sup> for DOC and 3000 mg C·m<sup>-2</sup> for TOC. Thus, the fluxes exceeded those at the control site by 2.5–11 times. During the last experimental stage, flux differences between the two manipulation plots diminished, and the flux values at both sites became similar. The probability value of the RIA indicated highly statistically significant differences between the infested plot and the control one ( $P < 0.0001$  for DOC;  $P < 0.0001$  for TOC).

Ecosystem input fluxes of carbon with bulk solution were less than 100 mg C·m<sup>-2</sup>, revealing only slight differences between the dissolved and particulate C fractions. The high values in bulk precipitation at the end of May probably resulted from pine pollen input. Samples taken on the first date in July were omitted because of external contamination (Fig. 2).

**Fig. 2.** Throughfall and bulk fluxes of (a) total organic C (TOC) and (b) dissolved organic C (DOC). Values are means, and error bars are SEs. The arrow indicates when the insecticide was applied.



In principle, the timing of throughfall fluxes of TN were similar to those reported for C. Both exhibited similar TN fluxes at the two experimental sites in April, increasing flux differences in May and peaking inputs in June to mid-July, a period in which TN fluxes under herbivory yielded up to 260 mg N·m<sup>-2</sup> compared with 140 mg N·m<sup>-2</sup> in the control. This difference is statistically significantly ( $P < 0.005$ ). Balanced flux quantities were observed for the rest of the study period (Fig. 3a).

Fluxes of DN compounds statistically increased under herbivory ( $P < 0.004$ ) but deviated slightly from the flux pattern observed for TN (Fig. 3b). In this case, the peak fluxes for both sites occurred early (May) following relatively dry weather conditions. Subsequent flux differences in June–July were less pronounced, as was also found for TN and for C.

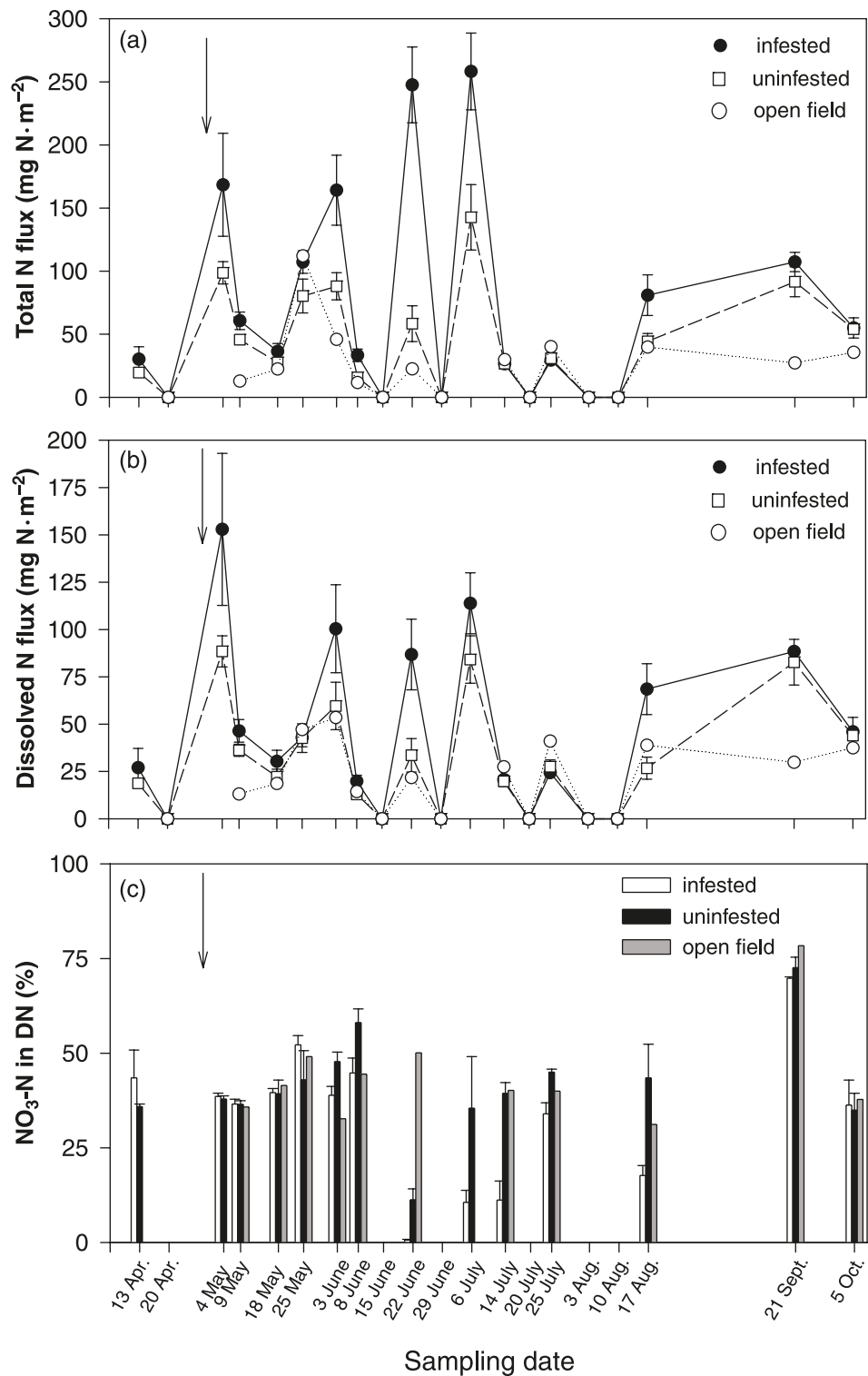
In the open field, input fluxes of N fractions with bulk solution ranged below 50 mg N·m<sup>-2</sup> (Figs. 3a and 3b), except for 25 May, where the doubled TN fluxes clearly were attributable to enhanced pollen deposition. Nevertheless, DN fluxes with bulk precipitation and with throughfall at the control site were sometimes quite similar and differ only by

a mean factor of 1.7, thus contrasting with the findings for the DOC dynamics, where open field fluxes were more than 6 times lower than the control ones.

#### Percentage of nitrate in DN in throughfall solution

The abundance of lepidopteron larvae not only affected the timing and quantity but, presumably, also the composition of DN compounds in throughfall (Fig. 3c). At the three sites, the percentages of NO<sub>3</sub>-N in DN were similar and ranged between 35% and 50% from April to the end of May. With increasing feeding activity, the proportion of NO<sub>3</sub>-N considerably diminished, with the lowest values (between 1% and 10%) occurring from late June to mid-July. This might indicate that herbivory immobilizes NO<sub>3</sub>-N in the canopy and, consequently, that DN consisted to more than 90% of NH<sub>4</sub>-N and residual N. Therefore, it distinctively differs from bulk and throughfall solution composition at the control site. The exceptionally high but similar NO<sub>3</sub>-N proportions of approximately 75% in September may result from the long sampling period and the probable progress of mineralization processes of accumulated organic matter in the solutions.

**Fig. 3.** Throughfall and bulk fluxes of (a) total N (TN) and (b) dissolved N (DN) and (c) percentages of NO<sub>3</sub>-N in DN in throughfall and bulk solutions at the three experimental sites. Values are means, and error bars are SEs. The arrow indicates when the insecticide was applied.

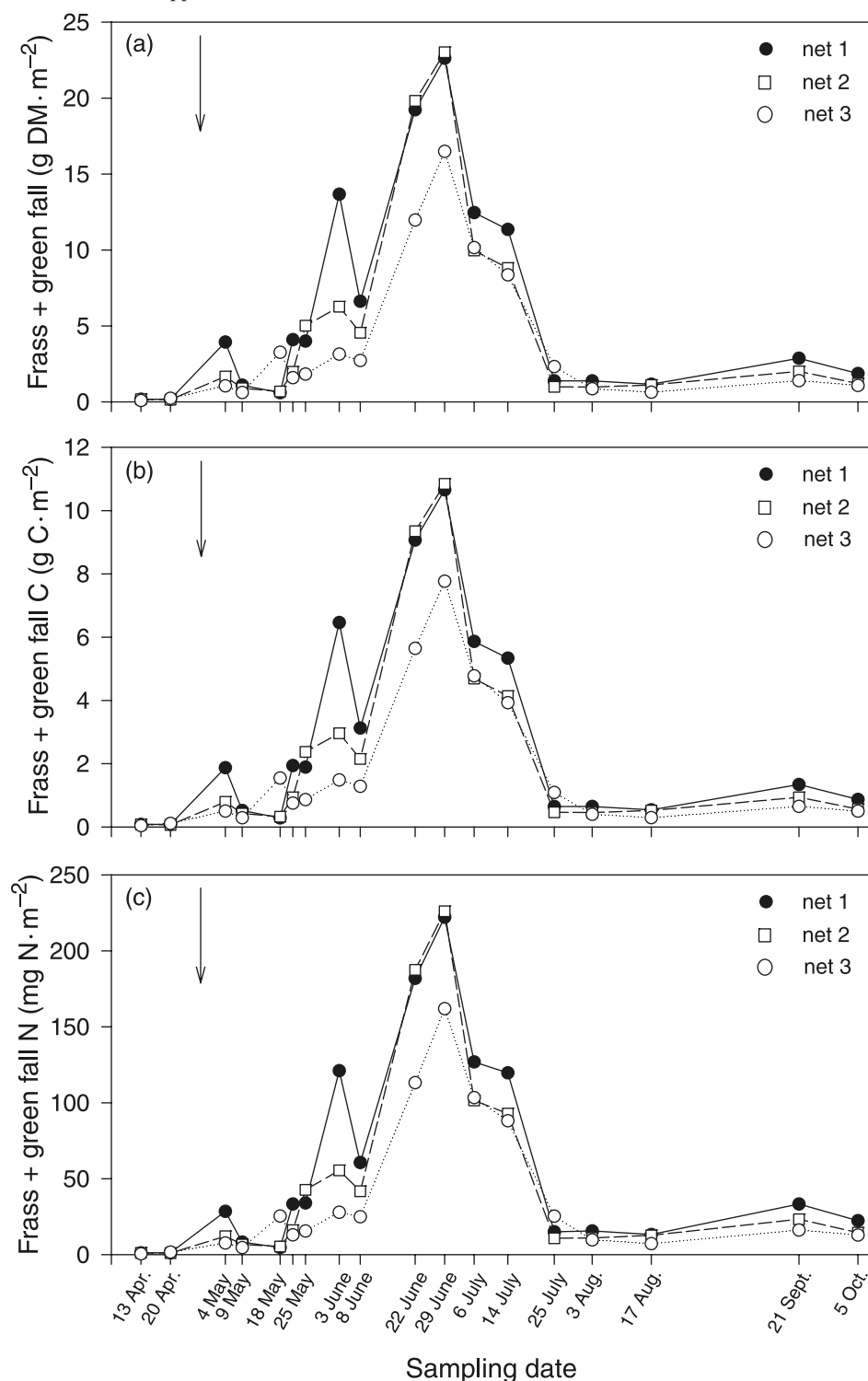


**Cumulative throughfall fluxes of C and N compounds**

Compared with the control, canopy herbivory more than doubled cumulative fluxes of TOC and DOC and by far exceeded those of bulk deposition. For N, the manipulation effects were slightly less pronounced showing TN quantities to be enhanced by 1.7 times and by 1.5 times for DN (Table 1).

On average, flux differences between the dissolved and the total fraction of C and N compounds were more distinct at the infested site than at the control and open site: under infestation, DOC only accounted for 77% of TOC and 62% of TN, whereas corresponding values at the control plot were 83% and 73%, respectively. With respect to PON (TN – DN),

**Fig. 4.** Fluxes of frass plus green-fall material as (a) quantities of dry matter (DM), (b) quantities of C, and (c) quantities of N. The arrow indicates when the insecticide was applied.



canopy herbivory probably triggers the production and transport of organically bound N from the canopy to the ground (Table 1).

From a quantitative point of view, organic C dynamics appeared to be more affected by herbivore infestation than N dynamics. This is also reflected by the mean POC (TOC – DOC) to PON ratio in throughfall solutions of the two ex-

perimental sites, where a higher ratio of 7.8 (more particulate organic carbon released than particulate nitrogen) was observed under herbivory than under noninfestation (ratio of 6.1).

#### *pH and electrical conductivity in throughfall solution*

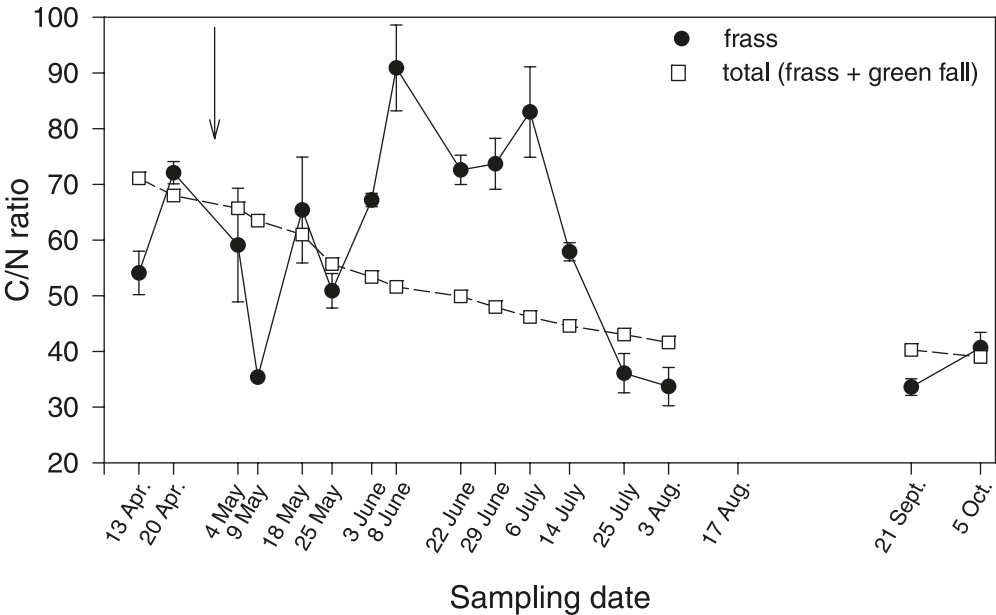
Values of pH and EC in throughfall solutions at the two experimental sites did not differ significantly (data not

**Table 1.** Cumulative fluxes of unfiltered and dissolved organic C and N with throughfall at the three experimental sites.

| Treatment  | Cumulative flux (kg·ha <sup>-1</sup> ·6 months <sup>-1</sup> ) |       |       |      |                    |      |
|------------|--|-------|-------|------|--------------------|------|
|            | TOC  | DOC   | TN    | DN   | NO <sub>3</sub> -N | PON  |
| Infested   | 180.4  | 138.0 | 14.06 | 8.69 | 2.92               | 5.37 |
| Uninfested | 81.4   | 67.6  | 8.24  | 5.99 | 2.35               | 2.25 |
| Open field | 17.6   | 11.1  | 4.00  | 3.43 | 1.46               | 0.57 |

**Note:** TOC, total organic C; DOC, dissolved organic C; TN, total N; DN, dissolved N; NO<sub>3</sub>-N, nitrate N; PON, particulate organic N.

**Fig. 5.** Mean C/N ratios in frass and total dry mass (frass plus green-fall material). Error bars for C/N ratios are SEs. The arrow indicates when the insecticide was applied.



shown). Throughfall solution pH under infestation was  $5.00 \pm 0.38$  (mean  $\pm$ SD),  $5.18 \pm 0.58$  under noninfestation, and  $5.70 \pm 0.58$  in bulk solutions. Similar values were also observed at the two forest sites for the EC:  $109 \pm 22$ ,  $99 \pm 30$ , and  $71 \pm 35 \mu\text{S}\cdot\text{cm}^{-1}$  in the infested, control, and open site, respectively.

**Carbon and N transfer by frass plus green fall**

Carbon and N inputs via frass plus green fall corresponded to the excretory activity of the phytophagous larvae, corroborating the flux dynamic pattern already observed for the element fluxes with throughfall (Figs. 2, 3, and 4).

The C and N contents of the frass plus green-fall material obtained from the nylon nets were quite similar, with standard deviations of  $<0.05\%$  for C and  $<1.5\%$  for N among the three replicates. Thus, the individually transferred C and N quantities per net very closely corresponded to the dry matter dynamics (Fig. 4a), yielding maximum weekly C fluxes with frass plus greenfall of up to  $10.6 \text{ g C}\cdot\text{m}^{-2}$  and N fluxes of  $230 \text{ mg N}\cdot\text{m}^{-2}$  during late June (Figs. 4b and 4c).

The C contents of the frass plus green-fall material remained relatively constant throughout the sampling period exhibiting values of approximately 47%, whereas the amount

of N continuously increased from 0.67% to 1.20%, which resulted in decreasing C/N ratios from 70 in April to 40 in October (Fig. 5). Carbon and N analyses on frass material only revealed a more heterogeneous picture: C/N ratios were approximately 55 in April and May, increased to 70–90 during June and early July, and decreased from August to October (Fig. 5).

The cumulative quantities of frass plus green-fall dry mass transferred from the canopy to the soil yielded to values between 680 and  $1090 \text{ kg}\cdot\text{ha}^{-1}$  dry mass, corresponding to mean C and N input fluxes of 420 and  $8.6 \text{ kg}\cdot\text{ha}^{-1}\cdot 6 \text{ months}^{-1}$ , respectively. Compared with the cumulative TOC and TN throughfall fluxes under canopy herbivory, mean C fluxes via frass plus green fall were found to be 2.3 times higher (418 compared with 180 kg C), whereas those of N were about 40% lower (8.55 compared with 14.1 kg N).

**Soil compartment**

**Soil contents of microbial biomass C and N ( $C_{\text{mic}}$  and  $N_{\text{mic}}$ ) and soil C/N**

The RIA revealed no significant effects of herbivory on soil microbial properties. Values for  $C_{\text{mic}}$ ,  $N_{\text{mic}}$ , and  $C_{\text{mic}}/N_{\text{mic}}$  ratios and soil C/N were nearly identical in the forest floor and the A horizon, respectively (Table 2). In general,



**Table 2.** Soil microbial parameters obtained from the forest floor and the Aeh horizon at the infested and uninfested site.

|   | Oh horizon       |                  | Aeh horizon     |                 |
|---|------------------|------------------|-----------------|-----------------|
|   | Infested         | Uninfested       | Infested        | Uninfested      |
| Microbial biomass C ( $\mu\text{g C}\cdot\text{g}^{-1}$ ) | 3205 $\pm$ 643   | 3104 $\pm$ 920   | 453 $\pm$ 129   | 557 $\pm$ 286   |
| Microbial biomass N ( $\mu\text{g N}\cdot\text{g}^{-1}$ ) | 376 $\pm$ 89     | 401 $\pm$ 165    | 55 $\pm$ 16     | 71 $\pm$ 37     |
| $C_{\text{mic}}/N_{\text{mic}}$                           | 8.8 $\pm$ 2.1    | 8.4 $\pm$ 2.6    | 8.5 $\pm$ 2.1   | 8.1 $\pm$ 1.9   |
| AEC   | 0.86 $\pm$ 0.03  | 0.86 $\pm$ 0.03  | 0.82 $\pm$ 0.05 | 0.83 $\pm$ 0.06 |
| ATP ( $\text{nmol}\cdot\text{g}^{-1}$ )                   | 11.22 $\pm$ 4.20 | 12.07 $\pm$ 4.69 | 2.56 $\pm$ 1.24 | 3.09 $\pm$ 1.48 |
| AMP ( $\text{nmol}\cdot\text{g}^{-1}$ )                   | 1.01 $\pm$ 0.54  | 1.00 $\pm$ 0.42  | 0.31 $\pm$ 0.12 | 0.33 $\pm$ 0.12 |
| ADP ( $\text{nmol}\cdot\text{g}^{-1}$ )                   | 1.74 $\pm$ 0.68  | 2.09 $\pm$ 1.03  | 0.59 $\pm$ 0.47 | 0.61 $\pm$ 0.23 |
| Total adenylates ( $\text{nmol}\cdot\text{g}^{-1}$ )      | 13.97 $\pm$ 4.96 | 15.16 $\pm$ 5.76 | 3.46 $\pm$ 1.48 | 4.03 $\pm$ 1.71 |
| ATP/ $C_{\text{mic}}$ ( $\text{nmol}\cdot\text{g}^{-1}$ ) | 3.61 $\pm$ 1.38  | 4.08 $\pm$ 1.72  | 5.72 $\pm$ 2.16 | 6.10 $\pm$ 2.44 |
| Soil C/N  | 31.9 $\pm$ 1.2   | 32.8 $\pm$ 1.4   |                 |                 |

**Note:** Values are means  $\pm$  SDs. AEC, adenylate energy charge.

forest floor contents of  $C_{\text{mic}}$  and  $N_{\text{mic}}$  were about six to seven times higher than in the underlying mineral horizon.

### Adenylate analyses

Indices characterizing the energetic status and activity of soil microbes, such as AMP, ADP, ATP, and ATP/ $C_{\text{mic}}$  ratios did not differ significantly among treatments (Table 2) except for the aAEC values in the forest floor (Fig. 6a). The probability value of the RIA test indicates differences between treatments close to statistical significance ( $P = 0.06$ ). Values for AEC ranging from 0.8 to 0.9 were predominantly found. This clearly indicates the presence of actively growing cells. Mean values of 0.82 and 0.83 were observed in the Ah horizon at both sites. On some reference dates, especially under infestation, values close to or  $<0.75$  (June 29) were observed. This indicates that the cells were nearly dormant and incapable of performing biosynthesis (Fig. 6b).

## Discussion

### Particulate and dissolved organic matter fluxes and quality

The temporal flux pattern that we observed for dissolved and unfiltered or particulate C and N compounds with throughfall suggest that they resulted from an interplay of different ecosystem processes. Unquestionably, C and N flux quantities are predominantly governed by the pine lappet's abundance and feeding activity (Lovett and Ruesink 1995), but also by precipitation patterns (allowing organic matter and nutrients to accumulate in the canopy during dry periods and to become remobilized during rewetting events; Mercier and Lindow 2000), external ecosystem deposition (e.g., pollen or inorganic N deposition), increased nutrient leaching from damaged leaves (Tukey and Morgan 1963; Stadler et al. 2001), and immobilization processes within the canopy mediated by phyllosphere microorganisms (Stadler and Müller 2000) probably contributed to the formation of distinct energy- and nutrient-transfer patterns.

Fluxes of DOC with throughfall in coniferous temperate forest ecosystems range between 80 and 160  $\text{kg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$  (Michalzik et al. 2001). Fischer et al. (1995) reported annual DOC throughfall fluxes between 82 and 97  $\text{kg C}\cdot\text{ha}^{-1}$  in three uninfested Scots pine stands in the eastern part of Germany. The value of 68  $\text{kg DOC}\cdot\text{ha}^{-1}$ , which we ob-

served at the control site over 6 months agrees reasonable well with this. However, the large semiannual DOC fluxes of 138  $\text{kg DOC}\cdot\text{ha}^{-1}$  under pine lappet herbivory clearly exceed known annual DOC throughfall fluxes and support the hypothesis of additional sources of organic matter in the canopy either by direct (excreta) and (or) indirect (leaching from damaged needle tissue) herbivore-mediated processes.

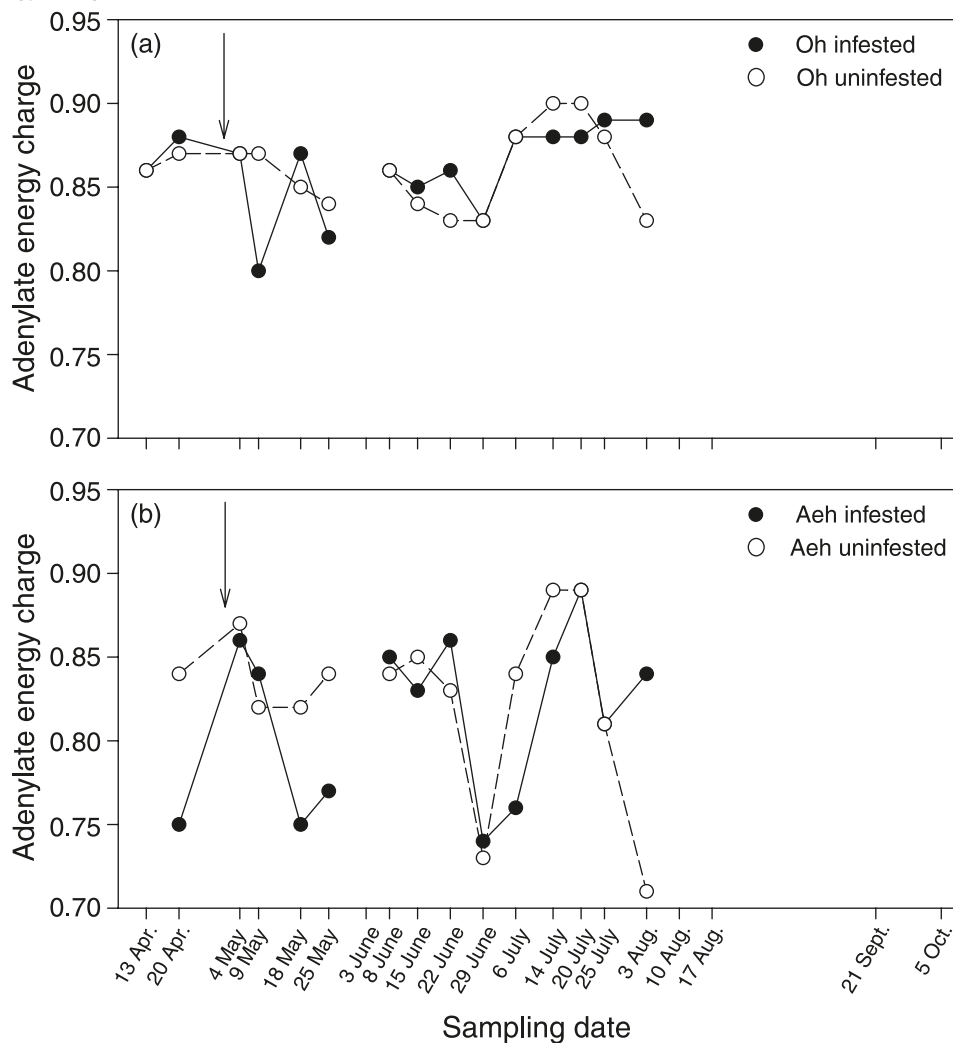
In unfiltered throughfall solutions, the fluxes of TOC under infestation amounted to 180  $\text{kg C}\cdot\text{ha}^{-1}$ , representing a mean of 40% of the frass plus green-fall C. This means that the frass and green-fall material entering the throughfall samplers only partly dissolved or decayed to form organic particles  $<500\text{ }\mu\text{m}$  in diameter. Consequently, approximately 60% of the frass plus green-fall derived material consists of organic particles  $>500\text{ }\mu\text{m}$ . This might have consequences for a further transport of this frass plus green-fall material from the forest floor surface deeper into the ground and subsequent degradation (mineralization) processes in the soil.

For the comparison of throughfall fluxes of dissolved and total C and N, only the study by Stadler et al. (2006), which analyzes the effects of hemlock woolly adelgids (*Adelges tsugae* Annand) infestation on vertical nutrient fluxes, provide comparable field data. In that case, the authors found enhanced DOC and DON fluxes (+24.6% and +28.5%, respectively) under adelgid infestation compared with the control, and significantly higher flux rates of TOC and total N (two to four times higher than the flux rates for dissolved ones) as well, especially during the early season.

Changes in the quality of throughfall chemistry under canopy herbivory with regard to N composition provide evidence for the trophic interaction with phyllosphere microorganisms immobilizing N in the canopy. In this case, the diminished percentages of  $\text{NO}_3\text{-N}$  in DN during highest feeding activity can probably be attributed to an enhanced growth of epiphytic microorganisms (bacteria, yeasts, and filamentous fungi). These organisms immobilize inorganic N in the presence of easily available C compounds that have been released from feeding-damaged needles as observed also by Stadler et al. (1998, 2001) and Lovett et al. (2002).

Promoted growth of phyllosphere microbial biomass under herbivore infestation might also contribute to observed enhanced flux amounts of PON and POC (size range 0.45–500  $\mu\text{m}$ ) by 140% and 67%, respectively. Because fil-

**Fig. 6.** Adenylate energy charge in the (a) forest floor (Oh) and (b) Aeh horizon. The arrow indicates when the insecticide was applied.



tration through a 0.45  $\mu\text{m}$  pore size excludes the majority of microbes (passing through a 0.2  $\mu\text{m}$  pore size is defined as “sterile filtration”), we suggest that the particulate fraction largely represents frass, plant debris, and microbial biomass, corroborating results found by other authors (Stadler et al. 1998; Stadler and Müller 2000).

#### Solid organic matter fluxes via frass plus green-fall material

With respect to leaf feeders, huge quantities of nutrients such as N, P, and potassium (K) are transferred back to the ground by solid matter inputs via frass, green needle debris, and insect biomass (Reynolds and Hunter 2001). According to Grace (1986) the overall input of returned nutrients rather than the timing of deposition is of importance. In a 60- to 80-year-old oak stand infested by gypsy moths (*Lymantria dispar* (L.)), Grace (1986) found that 67% of the N, calcium, K, magnesium, and P inputs already occurred during the vegetation period under herbivory and the rest in autumn, compared with the control site, where the majority (86%) of nutrients returned with litterfall in autumn and only 12% during the spring and summer months. In our study, the temporal dynamics of the organic matter inputs distinctly fol-

lowed the specific life cycle and feeding activity pattern of the pine lappet larvae. Consequently, peak fluxes occurred within a short period of 5 weeks during June–July: approximately 80% of the overall inputs enters the ground under herbivory, highlighting the significant altered timing of organic matter cycling.

Apart from altered quantities and timing of nutrient inputs, canopy herbivory also modifies the chemical quality and form of organic compounds (Swank et al. 1981). After passing through the digestive system of herbivorous insects, the organic material significantly differs from the former plant biomass: it contains more nutrients, has a higher biological activity, and thus, is more readily decomposable by soil microbes (Schowalter et al. 1986; Lovett and Ruesink 1995).

In our study, the N return by frass plus green fall (8.6 kg N $\cdot$ ha $^{-1}$ ) was considerably lower than that reported by Grace (1986) and was exceeded by total N input fluxes with throughfall (14 kg TN $\cdot$ ha $^{-1}$ ). This probably indicates a depletion of N in insect-processed frass material and corroborates the highly differing C/N ratios in the frass material with C/N ratios of 55 in April–May and up to 90 during peak larval abundance in June–July. In this case, we suggest

a pronounced assimilation of N by the moth larvae during needle biomass ingestion, thus enhancing the C/N ratios by means of a high N utilization efficiency as observed by other authors for the gypsy moth and different food qualities (Lovett et al. 2002; Giertych et al. 2005).

### Effects on soil microbial processes

To date, results testing the effects of biologically mediated enhanced input fluxes of organic matter on soil biological processes, such as mobilization and mineralization of soil organic matter, priming effects, lignin degradation, and long-term nutrient storage, are ambiguous (Guggenberger and Zech 1994; Michalzik et al. 2001). For example, Swank et al. (1981) reported significantly enhanced nitrate exports from a watershed following insect pest outbreaks, whereas Bormann and Likens (1979) found no such effects in the Hubbard Brook Experimental Forest. In laboratory experiments, Lovett and Ruesink (1995) observed an immobilization of N after faeces material was applied. No effects of faeces or green-fall application on C and N mineralization rates and litter decay were reported by Russell et al. (2004) or by Reynolds and Hunter (2001). Although remarkable differences with regard to the overall C and N input, the altered timing, and quality underneath defoliated and control trees occurred in this study, indices of microbial biomass and its energetic status in the soil showed no or only slightly significant responses. On the other hand, Streminska et al. (2002) recorded changes in the diversity and activity of soil microbes in a pine forest subsequent to an occurrence of lepidopterous larval herbivory, which caused a 60% loss of the canopy biomass. At the infested site, higher numbers of ammonifying and denitrifying bacteria and fungi were found. This was accompanied by enhanced N mineralization rates. With regard to the adenylyte analysis, the weak statistically significant difference found for AEC in the forest floor might indicate more actively growing cells benefiting from enhanced nutrient deposition and availability (Dinesh et al. 2004).

In view of these contradicting experimental results, other ecosystem state properties, such as the existing pool of organic matter and elements in the system and the nutrient supply and demand of the biosphere, might govern soil biological processes. In this context, manipulation experiments could test for system-specific "threshold inputs" of organic matter, which trigger effects on mineralization and mobilization rates.

### Conclusions and outlook

The results of our field experiment clearly support the hypothesis of effects exerted by the pine lappet on the biogeochemical cycling of energy and nutrient elements in a Scots pine stand. We examined novel pathways by which insect herbivores affect ecosystem processes, focusing on internal transfer fluxes especially of POM and concurrently followed their implications on soil microbial functional parameters presumably triggered by altered timing and throughfall chemistry, green-fall plus frass fluxes from the canopy to the ground. Weekly measurements on above- and below-ground processes, such as organic matter fluxes and indices of soil microbial functions, revealed highly dynamic patterns.

Our data suggest that herbivory-mediated production of organic matter in solid and especially in particulate and dissolved form contributes considerably to the overall input of organic substances into the soil compartment. Apart from modified quantities and forms of the organic matter, the timing of organic compounds delivered to the forest floor has to be stressed. Given that this pathway is rarely considered in ecosystem studies, gaps in element budgeting might be explained by including POM dynamics in future studies. This would also allow a better understanding of the interplay between above- and below-ground processes in ecosystems.

As stated by Rinker et al. (2001), only a few studies connect the canopy to ground processes and quantify interactions among canopy herbivores, soil fauna, and decomposition processes. We suggest that future research should focus on (i) quantifying the quantities, the quality, and the timing of herbivore-derived organic matter produced under different climatic and environmental conditions in comparison to other fluxes and pools of organic matter; (ii) the influence of POM on soil processes (e.g., priming effects, long-term nutrient storage, and plant–soil microbe competition); (iii) the occurrence of threshold values of organic matter entries triggering soil microbial responses; and (iv) the potential effects of climate change on biospheric feedback processes (e.g., herbivore population dynamics and leaf or needle quality).

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