Plant Soil (2009) 325:255–262
DOI 10.1007/s11104-009-9976-2

REGULAR ARTICLE

Canopy herbivory altering C to N ratios and soil input patterns of different organic matter fractions in a Scots pine forest

Anne le Mellec · Michael Habermann · Beate Michalzik

Received: 23 October 2008 / Accepted: 19 March 2009 / Published online: 8 April 2009

Abstract Herbivorous insects can affect ecological processes in forested ecosystems such as nutrient and matter cycling especially during outbreak situations. However, the knowledge about their contribution to the quality and flows of energy and matter in forests is still imperfect. In this paper we report on the herbivore-affected C to N ratios in different fractions of organic matter cascading from the canopy to the forest floor during a pine lappet (*Dendrolimus pini* L.) mass infestation. Throughout a four months period we monitored the C and N fluxes with throughfall, and the C/N ratios of insect excrements (faeces) and pine needles in an 80-year-old Scots pine forest. Compared to the control, herbivore defoliation significantly magnifies C and N input fluxes by two to three times amounting to 95 kg TOC and 5.9 kg TN ha^{-1} in addition. Concurrently NO_3-N fluxes diminished and the C/N ratios in throughfall solutions increased during peaking frass activity. Compared to fresh needle biomass, the C/N ratios in insect faeces triple during peaking frass activity resulting in values between 70 and 100. This study demonstrates the importance of herbivorous insect's pests on element cycling as they act as a short-time phenomenon altering the nutrient quality and quantity reaching the forest floor and potentially affecting below-ground processes.

Keywords C/N ratio · Pine lapper infestation · Scots pine · Throughfall fluxes · Pine needles · Insect faeces

Responsible Editor: Ingrid Koegel-Knabner.

A. le Mellec (✉)
LOEWE-Biodiversity and Climate Research Centre (BiK-F),
Georg-Voigt-Straße 16, Senckenberganlage 25,
60325 Frankfurt am Main, Germany
e-mail: amellec@gwdg.de

M. Habermann
NW-FVA Northwest German Forest Research Station,
Department B, Forest protection,
Grätzelstr. 2,
37077 Göttingen, Germany

B. Michalzik
Friedrich-Schiller-University of Jena,
Institute of Geography, Chair in Soil Science,
Löbdergraben 32,
07743 Jena, Germany

Introduction

Forested ecosystems are characterized by a high temporal and spatial variability in the vertical transfer of energy and matter from the canopy to the soil (McDowell and Likens 1988). There is growing evidence that organic matter inputs from the canopy considerably influence organic matter and nutrient dynamics in the forest floor (Levia and Frost 2006). By altering carbon mineralisation rates (Michalzik and Stadler 2000) or inducing priming effects

(Fontaine et al. 2004), those inputs might affect ecosystem processes and services such as nutrient availability and C sequestration (Cronan and Aiken 1985).

Searching for the origin of seasonal fluctuations in throughfall composition and fluxes, in most cases leaf leaching has been considered as the principle source of organic substances. However, the role of herbivorous insects and the ecological processes they initiate especially during outbreak situations received less attention in past times.

In this context, ecologists now emphasize the need for connecting biological processes occurring in different ecosystem strata to explain rates of nutrient cycling and ecosystem functioning (Bardgett et al. 1998; Schowalter 2000; Wardle et al. 2000). As recently pointed out by Stadler et al. (2006), field studies directly tracking altered inputs of organic matter and changes in throughfall composition during insect defoliation are difficult to conduct and hence scarce.

In temperate forests, the principle flow path of organic matter and associated nutrients from the canopy to the ground is provided by litter-fall amounting to annual C fluxes between 900 and 2,600 kg C ha^{-1} a^{-1} and 20 to 55 kg ha^{-1} a^{-1} for nitrogen (Michalzik et al. 2001). Secondly, organic matter and nutrients are returned to the soil by throughfall deposition achieving annual fluxes between 40 and 160 kg DOC ha^{-1} a^{-1} and 1.2 to 11.5 kg DON ha^{-1} a^{-1} (Michalzik et al. 2001).

Since element and nutrient fluxes are conventionally measured after standard filtration (0.45 µm pore size), the exclusion of the particulate/unfiltered organic matter fraction (0.45 µm < particulate organic matter (POM) < 500 µm) potentially results in misleading inferences and budgeting gaps when studying nutrient and energy fluxes in ecosystems (Michalzik and Stadler 2005). In this context, annual input fluxes as particulate organic carbon (POC) can exhibit fluxes of up to 227 kg C ha^{-1} a^{-1} (Carlisle et al. 1966).

The quality of leaf litter and organic material entering the soil is recognized as one of the most important factors in forest ecosystems for nutrient recycling and humus formation (Polyakova and Billor 2007; Kainulainen and Holopainen 2002). The quality of leaf litter differs with tree species (Lorenz et al. 2004) and with age class (Gora 1995). Litter biodegradation is determined by readily (soluble carbohydrates) and recalcitrant (alkyl C, cutin, waxes, lignin) organic compounds, as well as by secondary organic compounds (polyphenols, tannins) (Preston et al. 1997; Hättenschwiler and Vitousek 2000).

The C/N ratio of leaf litter has become one of the widely accepted predictor for the estimation of decomposition rates (Pérez-Harguindeguy et al. 2000; Waksman 1924). It is well documented that needle tissue from coniferous trees like pines usually has wider C/N ratios of 60–80 than leaf tissue of broadleaf trees like alder species for example showing values of 15 to 20 (Lorenz et al. 2004; Polyakova and Billor 2007). It is suggested that wider C/N ratios of > 30 tend to decelerate decomposition rates (Pérez-Harguindeguy et al. 2000). However, compared to fresh leaf biomass the effects of insect herbivory and associated frass activity on the quality and amount of digested and excreted leaf biomass (faeces) are rarely investigated in field experiments.

In this study we investigated the effects of a heavy pine lappet infestation on the amount and quality of C and N inputs from the canopy to the soil surface. By tracking the C and N fluxes with throughfall solution, and the C/N ratios of insect excrements and pine needles at the infested and uninfested control site of a pine forest stand, we aim to clarify the following questions. First, whether insect herbivory affect C and N dynamics uniformly and secondly, whether temporal patterns associated with the larvae's abundance and feeding activity are reflected in the amount of C and N throughfall fluxes and the quality of insect faeces.

Materials and methods

Site description

The study site is located in northern Germany in the "Wendland" area at an altitude between 60 and 100 m a.s.l. The climate is classified as sub-continental and has a mean annual precipitation of approximately 545 mm, and mean annual temperatures of approximately 8.6°C (German Federal Meteorological Service 1961–1990, Weather Station Lüchow).

The forest site forms part of the "Prezeller Forst" and is planted with Scots pine (*Pinus sylvestris* L.) evenly aged and approximately 80 years old, growing at stocking densities between 1,039 and 1,045 stems per hectare. Understory vegetation includes patches of grass, moss and fern vegetation.

The soil type is classified as a Haplic Podzol (WRB 2006) derived from glacial and aeolian sand deposits, forming a sandy AE horizon 8 to10 cm thick, followed by a Bhs horizon gradually transitioning into the underlying parent material. The humus layer is classified as a mor humus type being 5 to 7 cm thick encompassing a thin (< 1 cm) litter layer (Oi), a fermentated (Oe) and a thick (3–5 cm) humic (Oa) layer. The C content of the forest floor (mixed sample) was 42% at the infested 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_2O) of the forest floor at both sites is approximately 4.80, that measured in KCl 3.05.

Experimental set-up

The experimental monitoring covered a period of four months and started in early April and ended in mid-August 2005. It focused on the determination of C and N fluxes and forms in throughfall solution, fresh pine needles and insect faeces.

The two experimental sites covered similar areas of 1.65 and 1.96 ha and were both initially infested with comparable densities of the pine lappet moth (*Dendrolimus pini* L.). This pre-treatment phase in April lasted for approximately three weeks, until the control plot was cleared of moth larvae by helicopter spraying on April 30, 2005, when 75 g diflubenzuron (trade name Dimilin®, a caterpillar-targeting insecticide) per hectare were applied. The extent of the pine lappet mass outbreak on the infested site caused defoliation losses of up to 70%.

Throughfall was sampled by using open funnel samplers of 326 cm^2 sampling area, which were randomly established in 10 replicates each on the infestation and the control site covering an area of about 40 by 40 meters. Two throughfall samples were pooled to one sample, subsequently resulting in 5 throughfall samples per study plot and sampling date.

To collect insect frass deposits on the infestation plot three polyester nets with a mesh size of 300 by 300 µm were installed. Each net was stretched around one pine tree and was individually adjusted to the canopy diameter resulting in differing net areas between 6.5 and 7.2 m^2. Sampling was performed at 6 to 8 day intervals from April to early August covering the main infestation period. At the infested site, fresh pine needles from four trees were collected and pooled to one needle sample per sampling date.

Chemical analysis

Pine needles and insect faeces were dried at 45°C until weight constancy was reached, grinded and analysed for C and N contents by thermal oxidation (LECO, CHN−1,000).

One aliquot of the throughfall solutions was 0.45-µm membrane-filtered (Cellulose-acetate filters, Sartorius). The analysis included the determination of dissolved organic carbon (DOC) and dissolved nitrogen (DN) by thermal oxidation (Dimatoc 100, Dimatec, Essen, Germany), and NO_3^- by ion chromatography (761 Compact IC, Metrohm). In unfiltered aliquots, total organic carbon and total nitrogen (TOC and TN < 500 µm) were also assessed by thermal oxidation (Dimatoc 100, Dimatec, Essen, Germany). The upper particle size limit of 500 µm was determined operationally by the capillary diameter of the TOC/TN-analyser. Throughfall fluxes of C and N fractions were calculated from solution concentrations and corresponding water volumes per sampling date.

Since inorganic carbon (IC) was not detectable in throughfall solutions, DOC and TOC basically reflect total carbon in filtered and unfiltered solutions, respectively. In this context, the C/N ratios in solutions were derived from ratios between DOC (TOC) and DN (TN).

Differences between throughfall solutions and the C/N ratios between faeces and pine needles were tested with the Mann-Whitney U-Test, because of small sample sizes and partly non-normal distribution. All statistical analyses were performed by SPSS software version 12.0.

Results

Throughfall fluxes

Fluxes of DOC and TOC with throughfall at the infested site responded quickly to the presence of enhanced feeding and excreting activity of the pine lappet peaking between mid-June and early July

(Fig. 1a). In general, flux differences between the infested and control site were more pronounced for TOC (unfiltered throughfall solutions) than for DOC. During June, mean flux differences of DOC and TOC under infestation were up to 18.5 and 27.5 kg C ha^{-1} higher than those at the control site. Fluxes during larvae abundance from May to mid-July always significantly differed between control and infested trees for both DOC and TOC (Mann Whitney test: $P<0.01$ and $P<0.001$, June 22nd). By the end of July differences in DOC and TOC fluxes diminished to < 4 kg C ha^{-1} with lessening feeding activity and beginning pupation. During the study period of four months, the input of DOC and TOC under insect herbivory amounted to 111 and 153 kg C ha^{-1} and to 45 and 58 kg C ha^{-1} at the control site.

Fluxes of TN, DN and NO_3-N in throughfall exhibited a diverse response to the larvae development. Mean flux differences of NO_3-N were negatively affected by the pine lappet infestation, as controls tended to have slightly higher fluxes, resulting in negative values, particularly during peaking excreting activity in June and early July (Fig. 1b). Total nitrogen showed a stronger response towards the larvae feeding activity than dissolved nitrogen (DN), as reflected by the highly significant flux differences (Mann Whitney test: $P<0.001$) of up to 1.9 kg N ha^{-1} in June. By mid July, no significant flux differences of TN, DN and NO_3−N between the two treatments were notable. Cumulative N input fluxes over four months amounted to 7.3 DN and 12.4 kg TN ha^{-1} under insect herbivory corresponding to 4.7 and 6.8 kg N ha^{-1} at the control site.

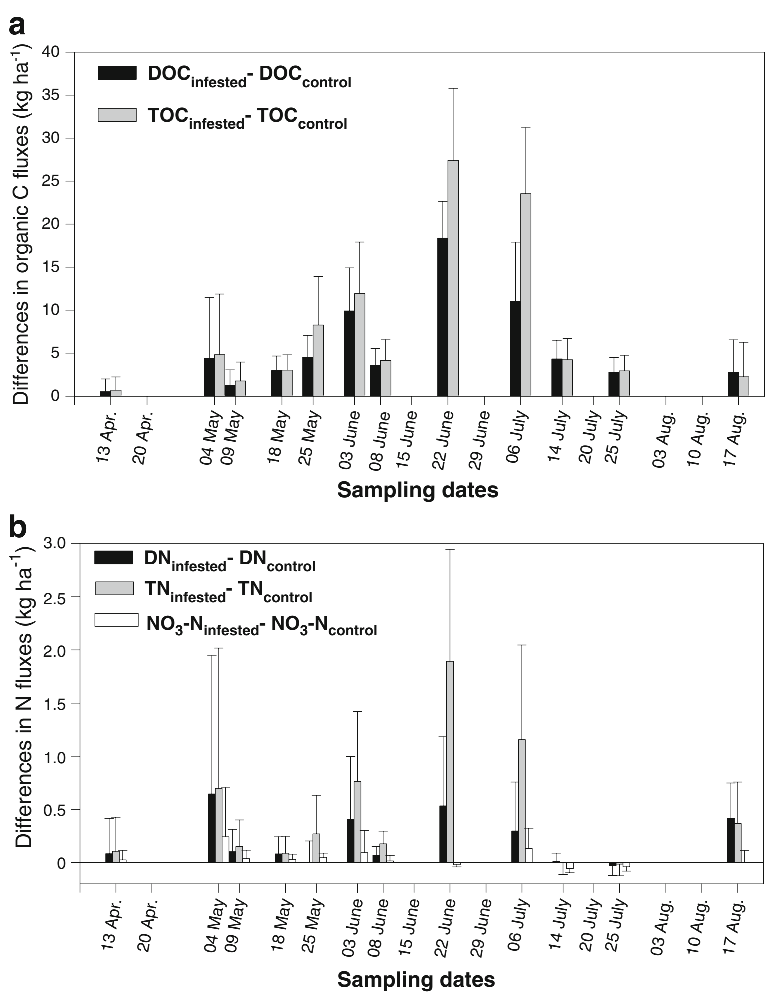

Fig. 1 Mean flux differences of filtered and unfiltered throughfall solutions between the larvae infested and unaffected control site with a) DOC and TOC mean flux differences (kg ha^{-1}) and b) DN, TN and NO_3-N mean flux differences (kg ha^{-1}). Error bars represent Gaussian random errors of measurements (error propagation)

C to N ratios in throughfall solution

To analyse for potentially decoupled C and N response to insect herbivory compared to the unaffected control, we tracked the C/N ratios derived from organic carbon (here equalling total carbon) and total nitrogen concentrations in filtered and unfiltered throughfall solutions over the course of the study (Fig. 2).

In April and early May, the C/N ratios in the two fractions (filtered/unfiltered solutions) of C and N at the infested and control site exhibited similar values between 5 and 7 (Fig. 2). With intensified feeding activity starting in mid-May, the C/N ratios in filtered and unfiltered solutions at the infested site started to widen to values around 15 to 20, while those of the control just slightly increased to 10. During peaking excreting activity during June und early July, C/N ratios in filtered solutions under infestation significantly differ from unfiltered ones (Mann Whitney test: $P=0.0029$), revealing values around 25 compared to 15, respectively. Concurrently, the two fractions at the control site exhibited similar C/N ratios between 5 and 10, which were significantly lower compared to the infested site (Mann Whitney test: $P<0.001$). Maximum C/N ratios of about 40 were achieved in mid-July under herbivory with similar values for both, the filtered and unfiltered fraction. With decreasing frass activity by the end of July and in August the C/N ratios of all fractions fell back to similar values between 10 to 17.

Pine needles and insect faeces composition

The C/N ratios of the pine needles were relatively constant throughout the course of the study, showing mean values between 34 and 40 (Fig. 3). Whereas, insect faeces exhibited highly variable C/N ratios with values of approximately 60 in April and May, contrasting the low temporal C/N variability of the pine needles. Widest faeces C/N ratios occurred during peaking frass activity of the larvae in June to mid July with maximum C/N ratios of 80 to 90. Differences in the C/N ratios between faeces and pine needles were significant at a P-level = 0.002 (Mann Whitney test). In principle, the patterns of faeces C/N ratio were reflected by those of the dissolved and total throughfall fractions as well, nevertheless, here the solution C/N ratios never exceeded values of 40 (Fig. 3). In August, differences between needle and faeces C/N ratios diminished to values of approximately 35, while those in throughfall solutions fell back to ratios of around 10.

Discussion

The knowledge about biological processes like herbivorous frass activity and their contribution to the quantity and quality of energy and matter is still imperfect. Only a few studies dealt with the role of herbivorous insects in the canopies of trees and their effects on the variability of concentrations and fluxes of organic carbon fractions and N composition in throughfall solution (Dighton 1978; Stadler et al. 1998).

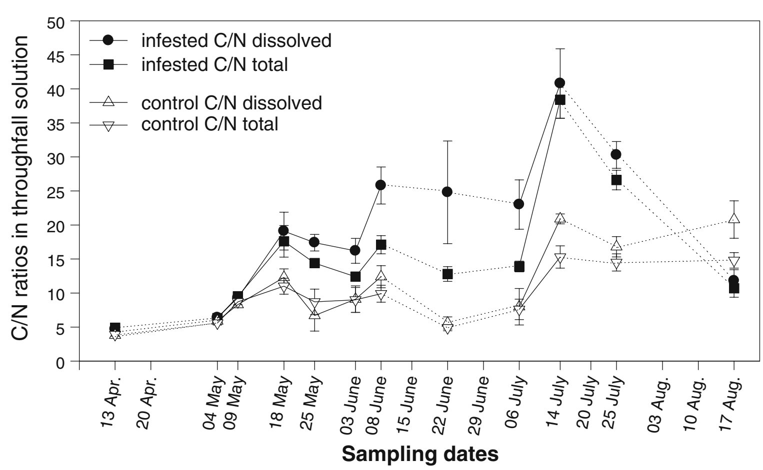

Fig. 2 C/N ratios in filtered (dissolved) and unfiltered (total) throughfall solutions at the larvae infested and uninfested control site (means ± standard error). For clarity in data presentation, dashed lines bridge sampling gaps due to absent rainfall

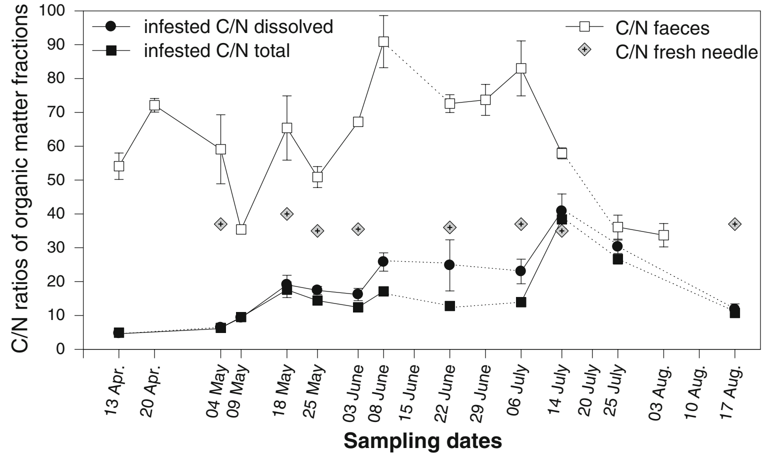

Fig. 3 C/N ratios in pine needles, insect faeces and filtered (dissolved) and un-filtered (total) throughfall solutions at the infested site (means ± standard error)

Throughfall solution

Fluxes of C and N with throughfall at the infested site clearly revealed patterns of associated herbivore excretion activity in the dissolved and especially in total C and N fraction, whereas the control ones generally exhibited lower matter fluxes, except for NO_3-N.

As a consequence, DOC and TOC fluxes accumulated over four months under infestation significantly surpassed those at the control site by two to three times, exhibiting values of 111 and 153 kg C ha^{-1}, which reach or even exceed most annual DOC throughfall fluxes ranging between 40–160 kg DOC ha^{-1} a^{-1} (Michalzik et al. 2001). Corresponding values for DN and TN fluxes under insect herbivory amounted to 7.34 and 12.43 kg N ha^{-1}, respectively.

The observations corroborate with findings by Stadler et al. (2001), who demonstrated that herbivore excretion alters throughfall solution by especially enhancing the organic C content and lowering inorganic N contents relative to uninfested trees. Stadler et al. (1998, 2001) hypothesized that changes in the quality of throughfall solution under canopy herbivory with regard to the N species composition supply evidence for the trophic interaction with phyllosphere micro-organisms immobilizing N in the canopy. In this case, the diminished fluxes of NO_3-N during highest feeding activity relative to the control can probably be attributed to an enhanced biomass growth of epiphytic micro-organisms (bacteria, yeasts, filamentous fungi) immobilizing inorganic N in the presence of easily available C compounds released from feeding-damaged needles as observed by Lovett et al. (2002) as well.

The C/N ratios in filtered (dissolved) and to a lesser extend in unfiltered (total) throughfall solutions under infestation clearly indicates decoupled C and N dynamics particularly during peaking feeding activity. This is likely due to the inorganic N immobilization in the canopy area described above together with a magnified release of dissolved C compounds from feeding-damaged needles and insect faeces. Furthermore, this probably indicates a depletion of N in insect faeces caused by 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 utilisation efficiency as observed by other authors for the gypsy moth and different food qualities (Lovett et al. 2002; Giertych et al. 2005).

C/N ratios in pine needles and insect faeces

The results on C/N ratios of pine needles compared to insect faeces showed a distinct temporal pattern due to varying assimilatory requirements of the larvae towards C and N nutrition associated with the single larvae development stages (Lunderstädt 1997; Lindroth and Bloomer 1991). Relative to C, pine needle tissue contains low N contents and therefore provides only small amounts of N for the larvae nourishment. Pine needle composition also depends on age classes and the conditions under which they grew up. In this context, Gora (1995) demonstrated, that age classes gowning up under high intraspecific conditions (less nutrient and water availability) exhibited favourable nutrient composition for defoliators containing less defence compounds, less starch content and higher contents of soluble sugar and amino acid in needles due to a disturbed tree physiology (Zwölfer 1963; Schwenke 1962, 1963).

In April the young and small-sized larvae started feeding on pine needles to cover the demand on required C (soluble carbohydrates) and N (proteins, amino acids) compounds for growth and metabolism processes (Lunderstädt 1997; Levinson 1976). In June/July highest frass activity by the larger-grown larvae occurred before they started pupation and oogenesis in July/August (Telang et al. 2001; Schwertdfeger 1981). At this time the widened C/N ratios of the insect faeces indicate a higher N over C demand, or a potential worsening of the C quality and a partitioning due to temporal changes of carbohydrates contents and forms in needles such as increasing indigestible starch contents resulting in a higher C accumulation in the excreta (Mandre et al. 2001; Waldmann 1999). This is reflected by the significantly increased C/N ratios in insect faeces compared to needle biomass. After pupation from August onwards the C/N ratios of insect faeces narrowed exhibiting similar values to those of the needle biomass.

Altered C/N ratios in herbivore-processed organic matter and potential impact on litter decomposability

Although the C/N ratio is an important indicator for assessing the decomposability of organic matter, it provides no information on the chemical quality of the organic material regarded. Organic matter revealing wide C/N ratios might contain high amounts of readily available carbon like soluble sugars associated with plant residues (Stevenson 1994), which might promote degradation processes by functioning as co-substrate potentially inducing priming effects (Fontaine et al. 2004). However, our study neither considered this fact nor analysed for chemical properties of the faeces material.

Nevertheless, with regard of its physical appearance we observed a quite inhomogeneous and porous surface of the pine lappet faeces, where the accessibility for microbial-mediated chemical and physical degradation activity would probably be more efficient compared to the cutin and wax protected intact pine needle surface. Furthermore, a significant proportion of the faeces easily dissolved in water, thus enhancing the reactive surface area and substrate accessibility for microbial degradation and the subsequent water transport into deeper soil layers. Due to a reduced substrate accessibility of intact needles, it might occur that needle biomass decomposition requires a higher number of trophic interaction and degradation steps among functional decomposer groups than those of faeces decomposers.

Conclusions

The study demonstrated, that insect mass outbreaks are capable to remarkably affect throughfall composition and fluxes within forest ecosystems. Consequently, insect infestations partly account for seasonal fluctuations observed in throughfall chemistry. From both a quantitative and qualitative point of view, our data suggest that the insect-mediated production of particulate and dissolved organic C and N considerably contributes to the overall input of organic substances from the canopy to the ground. However, this origin and pathway of canopy-derived organic matter is rarely considered in ecosystem studies and element budgets.

Acknowledgements We like to thank Ingobert Freitag and Werner Bodenstein from the Federal Office for Radiation Protection (BfS, Bundesamt für Strahlenschutz) for their support and kind permission to carry out this research study at forest sites within the “Prezeller Forst”. We are deeply indebted to Petra Voigt and Anja Soedje from the Laboratory Unit of the Institute of Geography at the University of Göttingen for chemical analyses and help during the study and to Annett Reinhardt for her great help in the field. Financial support was provided by the German Research Foundation (DFG, Project No. MI 927/1-3) and the German Ministry for Research and Technology (BMBF) supporting this research within the “Juniorprofessur” programme.

References

Bardgett RD, Wardle DA, Yeates GW (1998) Linking aboveground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. Soil Biol Biochem 30:1867–1878. doi:10.1016/S0038-0717(98)00069-8

Carlisle A, Brown AHF, White EJ (1966) The organic matter and nutrient elements in the precipitation beneath a sessile oak (*Quercus petraea*) canopy. J Ecol 54:87–98. doi:10.2307/2257660

Cronan CS, Aiken RG (1985) Chemistry and transport of soluble humic substances in forested watersheds of the

Adirondack Park New York. Geochim Cosmochim Acta 49:1697–1705. doi:10.1016/0016-7037(85)90140-1
Dighton J (1978) In vitro experiments simulating the possible fate of aphid honeydew sugars in soil. Soil Biol Biochem 10:53–57. doi:10.1016/0038-0717(78)90010-X
Fontaine S, Bardoux G, Abbadie L, Mariotti A (2004) Carbon input to soil may decrease soil carbon content. Ecol Lett 7:314–320. doi:10.1111/j.1461-0248.2004.00579.x
Giertych MJ, Bakowski M, Karolewski P, Zytkowiak R, Grzebyta J (2005) Influence of mineral fertilization on food quality of oak leaves and utilization efficiency of food components by the gypsy moth. Entomol Exp Appl 117:59–69. doi:10.1111/j.1570-7458.2005.00332.x
Gora V (1995) Physiologische Untersuchungen zur standort- und altersabhängigen Befallsdisposition von Kiefern- (Pinus sylvestris)-Beständen für nadelfressende Insekten. Cuvillier Verlag, Göttingen
Hättenschwiler S, Vitousek PJ (2000) The role of polyphenols in terrestrial ecosystem nutrient cycling. Trends Ecol Evol 15:238–243. doi:10.1016/S0169-5347(00)01861-9
Kainulainen P, Holopainen JK (2002) Concentrations of secondary compounds in Scots pine needles at different stages of decomposition. Soil Biol Biochem 34:37–42. doi:10.1016/S0038-0717(01)00147-X
Levia DF, Frost EE (2006) Variability of throughfall volume and solute inputs in wooded ecosystems. Prog Phys Geogr 30(5):605–632. doi:10.1177/0309133306071145
Levinson HZ (1976) The defensive role of alkaloids in insects and plants. Cell Mol Life Sci 32:408–411
Lindroth RL, Bloomer MS (1991) Biochemical ecology of the forest tent caterpillar: responses to dietary protein and phenolic glycosides. Oecologia 86:408–413. doi:10.1007/BF00317609
Lorenz K, Preston CM, Krumrei S, Feger KH (2004) Decomposition of needle/leaf litter from Scots pine, black cherry, common oak and European beech at a conurbation forest site. Eur J For Res 123:177–188. doi:10.1007/s10342-004-0025-7
Lovett GM, Christenson LM, Groffman PM, Jones CG, Hart JE, Mitchell MJ (2002) Insect defoliation and nitrogen cycling in forests. Bioscience 52:335–341. doi:10.1641/0006-3568(2002) 052[0335:IDANCI]2.0.CO;2
Lunderstädt J (1997) Die ökophysiologische Funktion von Insekten in Waldökosystemen aus forstlicher Sicht. Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie, Band 11, Heft 1–6, Bayreuth, pp 669–671
Mandre M, Tullus H, Kloseiko J (2001) Partitioning of carbohydrates and biomass of needles in Scots Pine canopy. Z. Naturforsch 57c:296–303
McDowell W, Likens GE (1988) Origin, composition and flux of dissolved organic carbon in the Hubbard Brook Valley. Ecol Monogr 58:177–195. doi:10.2307/2937024
Michalzik B, Kalbitz K, Park JH, Solinger S, Matzner E (2001) Fluxes and concentrations of dissolved organic carbon and nitrogen—a synthesis for temperate forests. Biogeochemistry 52:173–205. doi:10.1023/A:1006441620810
Michalzik B, Stadler B (2000) Effects of phytophagous insects on soil solution chemistry: herbivores as switches for the nutrient dynamics in the soil. Basic Appl Ecol 1:117–123. doi:10.1078/1439-1791-00017
Michalzik B, Stadler B (2005) Importance of canopy herbivores to dissolved and particulate organic matter fluxes to the forest floor. Geoderma 127:227–236. doi:10.1016/j.geoderma.2004.12.006
Perez-Harguindeguy N, Diaz S, Cornelissen JHC, Vendramini F, Cabido M, Castelanos A (2000) Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. Plant Soil 218:21–30. doi:10.1023/A:1014981715532
Polyakova O, Billor N (2007) Impact of deciduous tree species on litterfall quality, decomposition rates and nutrient circulation in pine stands. For Ecol Manage 253:11–18. doi:10.1016/j.foreco.2007.06.049
Preston CM, Trofymow JA, Sayer BG, Niu J (1997) ^{13}CCPMAS NMR investigation of the proximate analysis of fractions used to assess litter quality in decomposition studies. Can J Bot 75:1601–1613. doi:10.1139/b97-872
Schowalter TD (2000) Insect ecology: An ecosystem approach. Academic, San Diego
Schwenke W (1962) Neue Erkenntnisse über Entstehung und Begegnung von Massenvermehrung an Kiefer-und Fichtennadeln fressender Insekten. Z. ang. Ent 50:137–142
Schwenke W (1963) Über die Beziehung zwischen dem Wasserhaushalt von Bäumen und der Vermehrung blattfressender Insekten. Z.ang. Ent 54:101–107
Schwertdfeger F (1981) Die Waldkrankheiten: ein Lehrbuch der Forstpathologie und des Forstschutzes, 4th edn. Parey-Verlag, Hamburg, p 486
Stadler B, Michalzik B, Müller T (1998) Linking aphid ecology with nutrient fluxes in a coniferous forest. Ecology 79:1514–1525
Stadler B, Müller T, Orwig D (2006) The ecology of energy and nutrient fluxes in hemlock forests invaded by hemlock woolly adelgids. Ecology 87:1792–1804. doi:10.1890/0012-9658(2006) 87[1792:TEOEAN]2.0.CO;2
Stadler B, Solinger S, Michalzik B (2001) Insect herbivores and the nutrient flow from the canopy to the soil in coniferous and deciduous forests. Oecologia 126:104–113. doi:10.1007/s004420000514
Stevenson FJ (1994) Biochemistry of the formation of humic substances. In: Humus Chemistry: genesis, composition, reactions, 2.edn., Wiley, New York, pp 188–211
Telang A, Booton V, Chapman RF, Wheeler DE (2001) How female caterpillars accumulate their nutrient reserves. J Insect Physiol 47:1055–1064. doi:10.1016/S0022-1910(01)00085-3
Waldmann R (1999) Einfluss von Bestandesstruktur und waldbaulicher Behandlung auf die Entstehung großflächiger Massenvermehrungen nadelfressender Kieferninsekten am Beispiel der Nonne (*Lymantria monacha* L.) in Dauerschadgebieten des Niedersächsischen Tieflandes. Dissertation, University Göttingen
Waksman SA (1924) Influence of micro-organisms upon the carbon-nitrogen ratio in soil. J Agric Sci 14:555–562
Wardle DA, Bonner KI, Barker GM (2000) Stability of ecosystem properties in response to above-ground functional group richness and composition. Oikos 89:11–23. doi:10.1034/j.1600-0706.2000.890102.x
WRB (2006) World reference base for soil resources 2006. Food and agriculture organisation of the United Nations, Rome
Zwölfer W (1963) Über die Abwehreinrichtung unserer Waldbäume gegen Insektenschäden. Zeitschrift f. angewandte Entomologie 51:364–370