Agricultural and Forest Entomology (1999) **1**, 3–9

The impact of spruce aphids on nutrient flows in the canopy of Norway spruce

Bernhard Stadler and Beate Michalzik

Bayreuth Institute for Terrestrial Ecosystem Research, University of Bayreuth, 95440 Bayreuth, Germany

Abstract

1 This study investigated the effects of honeydew from aphids in the canopy of Norway spruce (*Picea abies* (L.) Karst.) on the nitrogen chemistry of throughfall using a rainfall simulation experiment. Throughfall collected beneath infested trees was compared with that from beneath uninfested trees, while standardizing the quality and quantity of the precipitation and plant age.

2 Honeydew excreted by *Cinara pilicornis* (Hartig) and *C. costata* (Zett.) significantly increased the concentrations of dissolved organic carbon (DOC) and hexose-C in throughfall. The average concentrations of nitrogenous compounds (NH_4-N, NO_3-N) in throughfall collected beneath infested trees were significantly lower than beneath uninfested trees.

3 Multiple regression analysis indicated that the amount of rain and NH_4-N concentrations were the best predictors of the concentrations of dissolved organic nitrogen (DON) in throughfall. Parameters that were closely associated with the level of infestation (DOC, hexose-C concentrations) did not have a direct relationship with DON. About 40% of the reduction in the concentration of DON in the throughfall was attributed to aphid–micro-organism interactions.

4 Particle amino nitrogen (PAN)-concentrations were highest under infested trees in July after aphid numbers had declined, indicating a concomitant decline in microbial biomass after honeydew becomes a limiting resource.

5 The comparison of the concentrations of different nitrogen compounds in throughfall of infested and uninfested trees indicated that aphids affect the carbon and nitrogen cycles in the phyllosphere by providing energy that fuels the metabolism of the micro-organisms. These processes seem to occur very rapidly.

6 We discuss the significance of the results and the prospects of linking the ecology of micro-organisms and herbivores with flows of nutrients through the canopy of trees.

Keywords Aphids, carbon–nitrogen cycles, *Cinara*, forested ecosystems, herbivore–micro-organism interactions, Norway spruce, phyllosphere ecology.

Introduction

Nutrient cycles are usually depicted as biomass production, storage and decomposition, occurring in separate compartments (Apps & Price, 1996; Townsend & Rastetter, 1996; Asner *et al.*, 1997). Thus, the interaction between C and N cycles typically involve above and below ground processes. The transformation of nutrients within a particular compartment, like the canopy of forest trees, e.g. via the feeding activity of herbivores and micro-organisms, is less apparent, although there is growing experimental evidence that micro-organisms affect plant–herbivore interactions (Benedict *et al.*, 1991; Krischik & Jones, 1991) and modify herbivore-based cycling of nutrients within ecosystems (Seastedt & Crossley, 1984; Schowalter *et al.*, 1986; Choudhury, 1988; Pastor *et al.*, 1993; Huntly, 1995). Aphids on Norway spruce provide carbohydrates for other organisms by excreting copious quantities of honeydew, which is rich in saccharose, glucose or fructose (for a review see Maurizio, 1985). Zoebelein (1954) and Zwölfer (1952) reported that *Cinara* spp. produced between 400 and 700 kg honeydew/ha/y in coniferous forests.

Correspondence: Bernhard Stadler. Fax: + 49 (0)921 55 5799.
E-mail: bernhard.stadler@bitoek.uni-bayreuth.de or
beate.michalzik@bitoek.uni-bayreuth.de

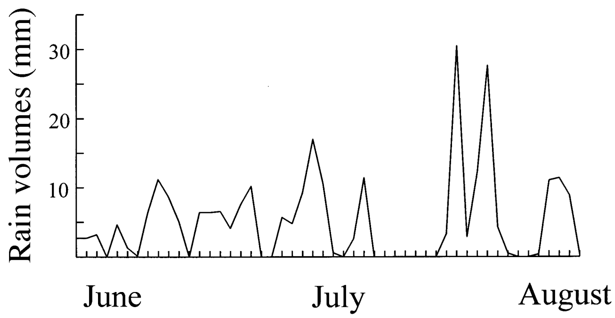

Figure 1 Quantities of rain applied to infested and uninfested Norway spruce. Irrigation schedules followed the records of rain for 1996 at the Waldstein site/Fichtelgebirge, Germany.

Thus, it is likely that aphids are important components of spruce forests and affect energy driven processes. These aphids are characterized by a clumped distribution on a few Norway spruce trees during spring and an almost even distribution during summer, after dispersal (Scheurer, 1964; Stadler *et al.*, 1998). When abundant, many aphid species can substantially reduce the growth of their host plants (Johnson, 1965; Dixon, 1971a, Llewellyn, 1975), resulting in a considerable loss in biomass. In the presence of honeydew, phyllosphere micro-organisms show increased population growth. A previous field study (Stadler *et al.*, 1998) revealed a two to three orders of magnitude increase in the abundance of bacteria, yeast and filamentous fungi on needles of Norway spruce, depending on aphid population size, season and the quantities of honeydew excreted. Thus, micro-organisms in the phyllosphere of Norway spruce seem to be energy limited. As these micro-organisms are able to metabolize inorganic N sources (Stadler & Müller, 1996), we hypothesize that they affect nutrient cycles in the canopies of trees. In particular, the presence of honeydew influences the concentrations of organic and inorganic nitrogen compounds in throughfall collected beneath spruce. Furthermore, if the C and N cycles are coupled via the phyllosphere the interactions between these cycles should occur very rapidly compared to nutrient cycles that involve above and below ground processes.

Dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) make up a substantial proportion of the total C and N in the throughflow of forest ecosystems. In the case of DON it can reach 25–50% of the total N in throughflow of deciduous forests (Matzner, 1988; Qualls *et al.*, 1991). Fluxes of DOC in throughfall may account for 74% of the above ground carbon fluxes in deciduous forests (McDowell & Likens, 1988) and 59% in coniferous forests (Manderscheid & Göttlein, 1995). However, it is unclear to what extent foliar leaching (Tukey, 1970; McDowell & Likens, 1988) and interactions between organisms in the canopies of trees influence throughfall chemistry. There is no indication that DON is a methodological artefact, produced by the biological transformation of substances in precipitation samplers (Michalzik *et al.*, 1997).

The objectives of this paper were to study by means of controlled aphid infestations and simulated rainfall whether: (1) honeydew affects the inorganic nutrient cycles in the canopy of spruce, (2) organic compounds, like DON, are a biological input into forests, i.e. $N_{mineral}$ is converted to $N_{organic}$ by means of biological processes that occur in the phyllosphere fuelled by aphid honeydew, or (3) organic compounds are an output from the canopy resulting from leaf leaching or leaf washing. This was studied by monitoring changes in the concentrations of substances in throughfall collected beneath differently aphid-infested trees during summer. The results are discussed in terms of the potential role of herbivores in forest nutrient dynamics.

Materials and methods

To standardize our investigations in terms of age of trees, nutritional supply, patterns of infestation, and amount of rain we designed a semi-natural rainfall simulation experiment. Six 10-year-old spruce trees (*Picea abies* (L.) Karst.) were covered with a transparent roof (20 m^2) in a field close to the university. All trees were obtained from a nursery and grown in containers 50 cm in diameter, 30 cm deep, filled with compost. To facilitate an increase in aphid abundance and honeydew production, three of the trees, after initial infestation with aphids, were enclosed in an insect-proof net (mesh size 1 mm), while the other three trees were kept free of aphids by an identical cage. Above each tree a semi-automated irrigation system was installed to spray 'rain' onto the trees with the help of a fine axial flow-full cone nozzle (Lechler, Metzingen), which released water at a 60° angle and a pressure of two atmospheres. The drizzle period was 9 s and the number of periods was determined by the volume of rain that had to be applied according to previous years' precipitation record. Rain was applied between 09.00 and 18.00 hours. Because the volumes and timing of the rain sprayed onto the trees were considered important parameters, which might affect our results, the quantities of rain applied followed the daily rain volumes recorded from June to August at the Waldstein site the previous year (Fig. 1). The Waldstein site is located in the Fichtelgebirge in north-east Bavaria/Germany at an altitude of 800 m a.s.l. where many biogeochemical processes and fluxes are measured routinely (see Stadler *et al.*, 1998, for further details). Thus, we used information on actual rainfall as a guide for our rainfall simulation experiment. For technical reasons it was not possible to use the records of the same year. The rain solution contained the following compounds (mg/L): 10.03 NH_4-N, 10.18 NO_3-N, 11.33 K_2SO_4, 3.55 Na_2SO_4, 4.93 $MgSO_4 \times 7H_20$, 7.33 $CaCl_2$, and 286.2 μg/L H_2SO_4 (1N) at pH 3.61. This solution has the same composition as the throughfall collected at the Waldstein site (e.g. in April/May 1996). The overall mean volume of rain was 5.3 ± 6.7 mm/day (mean ± SD).

At the beginning of May each of three of the trees was infested with 100 individuals of *Cinara pilicornis*, which feed on 1- and 2-year-old twigs and 100 *C. costata*, which feed on older twigs closer to the trunk. After the aphid populations peaked at the beginning/mid-July the insect netting that made up the side walls of the cage was removed to give natural enemies access to the aphid populations. Winged aphids were also able to disperse. Thus, the field situation was simulated with spruce trees heavily infested with aphids during June and declining aphid numbers from mid-July, which corresponds to the infestation pattern recorded for heavily infested trees at the Waldstein site (Stadler *et al.*, 1998). The nets that separated

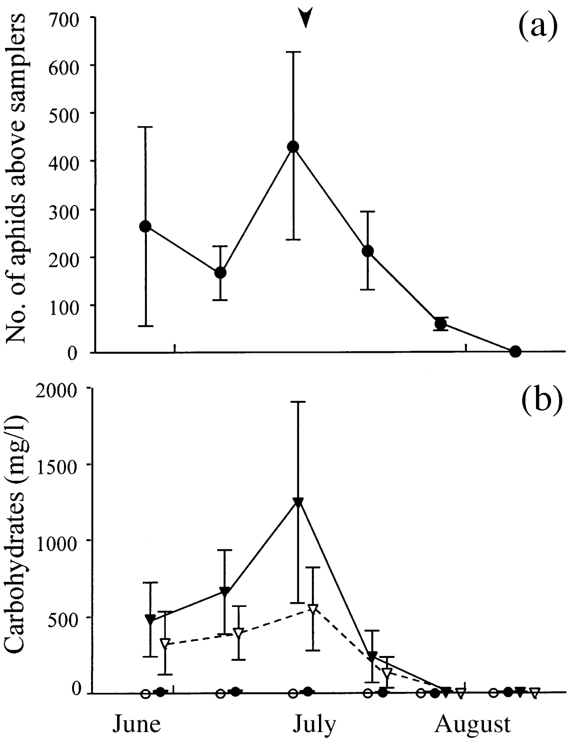

Figure 2 (a) Number of aphids above throughfall samplers during the experimental period (means ± SE), (b) dynamics in throughfall carbon concentrations collected in samplers underneath infested trees (DOC, ▼, solid line; hexose-C, ▽, dashed line) and uninfested trees (DOC, ●; hexose-C, ○) (means ± SE). The arrow indicates the time when the insect netting was removed.

the aphid-infested from the uninfested trees were left, which prevented the aphid colonization of the control trees.

Two rain samplers were placed underneath each tree, one close to the periphery of the canopy, the other close to the trunk to sample the spatial variability in throughflow chemistry. Each week throughfall was collected, the rain samplers were replaced and the number of aphids above each sampler was estimated. The funnel outlets of the throughfall samplers were plugged with a coarse filter to prevent needles or dead aphids from dropping into the reservoir. During the experiment the position of these samplers was not changed. Thus, it is possible that the C and N concentrations in the throughfall were affected by the aphids changing their feeding sites early in the season. However, not moving the samplers during the experiment reduced the effect of differences in the spatial pathways of water flows along needles and twigs affecting the quantities of throughfall collected.

Chemical analyses

Throughfall solutions were filtered immediately through a cellulose-acetate membrane (0.45 µm, Sartorius, Göttingen, Germany). DOC was determined as CO_2 after persulphate-UV-oxidation (Foss Haereus liqui TOC, Hanau, Germany) and hexose-C was measured colorimetrically by the anthrone method (Jermyn, 1975) at a wavelength of 630 nm. Ammonia nitrogen (NH_4-N) and NO_3-N were measured by ionchromatography (Dionex, Idstein). DON was calculated by subtracting NH_4-N and NO_3-N from total dissolved nitrogen. Particle-bound amino nitrogen (PAN) in unfiltered throughfall was measured colorimetrically by the ninhydrin method. Because ammonia reacts with ninhydrin, it was first removed by alkalization with 13.5 N NaOH and heating for 30 min at 60°C (ratio of sample solution: 13.5 N NaOH was 1.5 mL: 0.3 mL). The alkaline solutions were hydrolized at 100°C for 2 h. The samples were then measured at 570 nm after the ninhydrin reaction was complete (modified after Allen, 1981). According to Joergensen & Brookes (1990), the ninhydrin-reactive N provides a rapid and sensitive estimate of soil microbial biomass. Here it was used to indicate the microbial biomass dislodged from the phyllosphere by the throughfall.

A rigorous statistical treatment of the data is difficult if the data points are not independent of each other, which might apply here, especially at times of high aphid densities and low rainfall. The differences in the nutrient concentrations in the throughfall collected beneath infested and uninfested trees were tested using the Wilcoxon test of the mean value for the rain samplers on a particular date. Thus, the unit of comparison is not individual trees but averages from three trees (six data points per treatment per sample date). Because the origin of DON was of particular interest we used a multiple regression analysis to estimate the association of different explanatory variables with the concentration of DON as the dependent variable. Stepwise procedures were omitted (James & McCulloch, 1990).

Results

During June–July the aphid populations increased on the experimental trees, and individuals of both species of *Cinara* were clustered in dense colonies on different twigs, resulting in parts of the canopy being densely populated and others uninfested. Thus, the numbers of aphids above the rain samplers varied greatly especially at the beginning of the experiment (Fig. 2a). With the development of the current year shoots *C. pilicornis* dispersed and infested almost every new shoot at that time. Aphids were most numerous at the beginning/mid-July prior to the removal of the insect netting. Following its removal aphid populations started to decline due to dispersal and activity of natural enemies, which fed on the abundant aphids. At the beginning of August few aphids remained on the trees. The concentrations of DOC and hexose-C in throughfall collected beneath infested trees followed the trend in the abundance of aphids (Fig. 2b). Beneath uninfested trees there were no seasonal trends in DOC and hexose-C concentrations. Average concentrations in the throughfall collected beneath control trees were significantly lower with respect to DOC and hexose-C, but higher in NH_4-N and NO_3-N (Table 1). Differences in DON-concentrations did not differ significantly.

The seasonal trends in the concentrations of the different nitrogen compounds are given in Fig. 3(a–c). In throughfall collected beneath both infested and uninfested trees, DON concentrations were highest in mid-July and lowest in June and at the end of July/beginning of August (Fig. 3a). The availability of honeydew on infested trees was associated with generally lower DON concentrations. NH_4-N concentrations of through-

	Infested trees		Control trees			
	Mean ± SD	*n*	Mean ± SD	*n*	*z*	*P*
DOC (mg/L)	419.03 ± 856.91	6	11.51 ± 6.68	6	− 1.992	0.046
Hexose-C (mg/L)	198.26 ± 377.00	6	2.78 ± 1.65	6	− 1.992	0.046
DON (mg/L)	3.66 ± 2.81	6	5.92 ± 3.92	6	− 1 572	0.116
NH_4-N (mg/L)	8.57 ± 4.89	6	15.30 ± 3.87	6	− 1.992	0.046
NO_3-N (mg/L)	15.77 ± 5.81	6	20.87 ± 6.26	6	− 1.992	0.046

Table 1 Concentrations of carbohydrates (DOC, hexose-C) and nitrogen compounds (DON, NH_4-N, NO_3-N) in throughfall collected underneath infested and uninfested Norway spruce. *P*-values give the level of significance for differences between treatments (infested vs. control trees), Wilcoxon-test for paired samples.

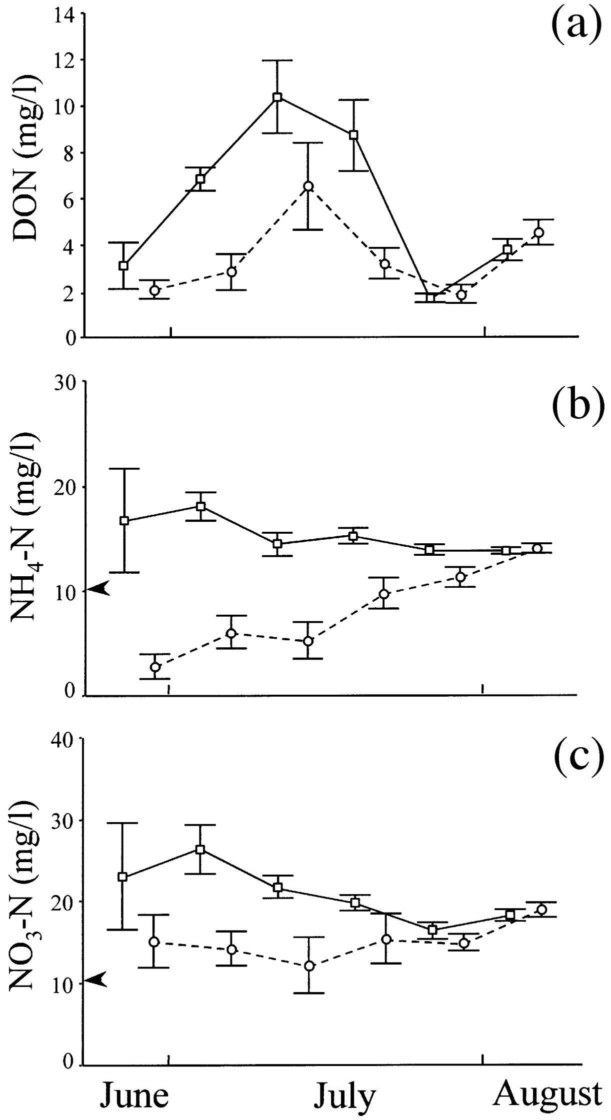

Figure 3 Seasonal change in concentrations of different nitrogen compounds collected in throughfall beneath infested (○, dashed line) and uninfested (□, solid line) Norway spruce (means ± SE). (a) Dissolved organic nitrogen (DON), (b) ammonia nitrogen (NH_4-N), (c) nitrate nitrogen (NO_3-N). Arrows indicate the concentrations in the artificial rain.

fall from infested trees increased with the decline in aphid populations from mid-July and was similar to that observed for uninfested trees in August (Fig. 3b). There were no pronounced seasonal trends in NO_3-N concentrations in the throughfall collected under aphid-infested and uninfested trees (Fig. 3c). The concentrations of all nitrogen compounds (DON + NH_4-N + NO_3-N) were consistently lower in solutions collected under infested trees than under uninfested trees so long as aphids were present, and differences in the concentrations disappeared at the end of the experiment. Average concentrations, over the complete study period, of DOC and hexose-C were 97.4 and 98.8% higher in throughfall collected under infested trees, respectively, whereas that of DON, NH_4-N and NO_3-N were 40.5, 46.2 and 27.5% lower, respectively. Only the concentrations of NH_4-N collected under infested trees (Fig. 3b) remained below the concentrations of inorganic N-compounds in the artificial rain, which indicates a selective uptake of ammonia and evaporation. Concentrations of PAN (an indicator of microbial biomass) were significantly higher in the throughfall collected beneath infested compared to uninfested trees from mid- to end of July, shortly before and after the removal of the lateral walls of the cages (Wilcoxon-test: $Z = -2.547$, $P = 0.011$, $n = 9$; Fig. 4).

A multiple regression analysis, with DON as the dependent variable, indicated that there was no direct or short-term effect of aphid numbers on the concentrations of organic N in throughfall, because neither of the variables associated with the presence/absence of aphids (treatment, or number of aphids above the samplers) had a significant effect (Table 2). Similarly, chemical parameters, which are correlated with aphid number (DOC, hexose-C), had no significant effect on DON concentrations. The best predictors of DON concentrations in throughfall were the concentrations of NH_4-N in throughfall and the volume of rain collected. Similar results were obtained when only infested trees were analysed or when the number and set of variables included in the analyses were varied.

Discussion

There is growing evidence that herbivores influence biogeochemical processes and have lasting effects on ecosystem structure (Ohmart *et al.*, 1983; Romme *et al.*, 1986; Huntly, 1991; Pastor *et al.*, 1993) and functioning (Swank *et al.*, 1981; Schowalter *et al.*, 1986; Choudhury, 1988; Grier & Vogt, 1990; Huntly, 1995). Aphids facilitate the transfer of plant photosynthates to the phyllosphere via honeydew, which consists mainly of sugars. The quantity of excreta can amount to 30 kg (fresh mass) from a single 70–80-year-old spruce tree during

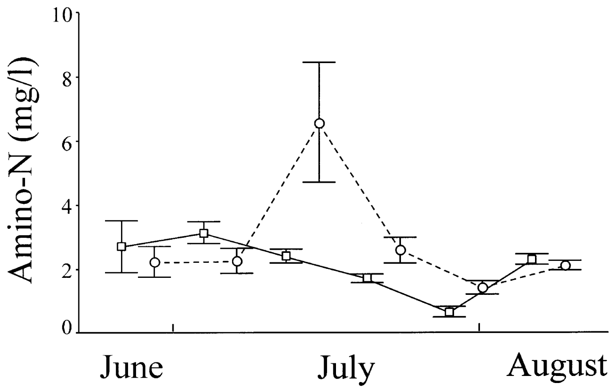

Figure 4 Seasonal dynamics in particle-bound amino nitrogen (PAN) concentrations in throughfall collected beneath infested (○, dashed line) and uninfested (□, solid line) trees (means ± SE).

Table 2 Multiple regression analysis with log-transformed DON concentrations in throughfall as the dependent variable and several parameters related to aphid infestation (treatment: infested; number of aphids above samplers) and throughfall chemistry as independent variables.

DON Source	B	SE	*P*
Treatment	−0.0527	0.084	0.531
Aphid number	0.0004	0.000	0.852
Volume (ml)	0.0005	0.000	0.005
Conductivity (µS/cm)	0.0007	0.000	0.040
DOC (mg/L)	0.0002	0.000	0.446
Hexose-C (mg/L)	−0.0002	0.001	0.744
NH_4-N (mg/L)	0.0494	0.012	< 0.000
NO_3-N (mg/L)	−0.0173	0.010	0.095
Constant	0.171	0.236	0.473

$F = 7.636$, d.f. = 8, $P < 0.0001$, $R^2 = 0.52$.

summer (Zoebelein, 1954; Müller, 1956), providing locally abundant energy in an otherwise energy-limited habitat. Micro-organisms often respond rapidly and efficiently to changes in availability of resources (Dik *et al.*, 1991; Krischik & Jones, 1991). Honeydew is known to cause an increase in the population densities of micro-organisms (bacteria, yeast, filamentous fungi) of between two to three orders of magnitude (Stadler & Müller, 1996). Thus, it seems likely that the availability of carbohydrates limits the abundance of micro-organisms in the phyllosphere of Norway spruce.

Our results indicate that the relationship between aphids and micro-organisms considerably affects the organic and inorganic chemistry of throughfall in Norway spruce forests. The carbohydrate concentrations were closely linked to aphid numbers and mirrored the infestation pattern. On infested trees, DOC concentrations were highest in July when aphid population densities were highest and declined thereafter (Fig. 2b). The average concentrations of C compounds in throughfall collected under infested trees were greater, but that of N compounds generally lower (Table 1, Fig. 3a–c). Because NH_4-N is the preferred N source for micro-organisms (Brock & Madigan, 1991) this result might indicate that micro-organisms thrive when honeydew is abundant. For example, it is conceivable that N compounds (especially NH_4^+) were used for microbial growth as long as carbohydrates were available (Figs 2b, 3b). With the fall-off in the supply of honeydew microbial population numbers declined, possibly with many micro-organisms dying or washed off, or both. This might account for the higher concentrations of PAN in the samplers beneath infested spruce during July. To date, there is no indication that the concentrations of organic and mineral nitrogen is significantly influenced by microbes washed into the throughfall samplers, even when much longer sampling periods are used (Michalzik *et al.*, 1997). There is no simple link between the honeydew of aphids, micro-organisms in the phyllosphere, and the organic N fraction in throughfall (Table 2). For example, DON concentrations rose and fell in July both under infested and uninfested trees (Fig. 3a), which seems to favour nutrient leaching (Tukey, 1970; Qualls *et al.*, 1991) at least during a particular stage in the foliar-cycle of spruce. Another source of DON might be the micro-organisms in the phyllosphere, which are likely to die and break up to PAN/DON when the supply of honeydew ceases. This might be indicated by the high amino-N concentrations in throughfall collected underneath infested trees during July (Fig. 4).

As very little is known about the interactions between aphids and micro-organisms during the course of a complete season or under different abiotic conditions in the phyllosphere of spruce, these aspects would deserve closer inspection. Carroll (1979) estimated the total volume of microbial cells on needles of a single old-growth Douglas fir to be 1093 cm^3, which would yield a biomass of 38–60 kg/ha. Our field results indicate that these figures are likely to increase substantially if carbohydrates become available (Stadler & Müller, 1996), and would subsequently affect the chemistry of throughfall and eventually the soil biota. The fact that the positive effect of honeydew on microbial growth in the phyllosphere is largely unseen does not preclude its importance. In addition to the effect of the excreta of aphids on throughfall, this study has shown that greater attention should be directed to understanding the biological interactions that influence throughfall chemistry other than foliar or needle leaching, because considerable amounts of nutrients enter the forest floor via throughfall (McDowell & Likens, 1988; Qualls *et al.*, 1991).

Except for the NH_4-N in throughfall collected beneath infested spruce, the concentrations of other inorganic N compounds were higher than those in the artificial rain. This indicates that evaporation reduced the volumes of rain collected, most likely at times when little artificial rain was applied. However, this is unlikely to affect the interpretation of our results because we compared the throughfall of infested with uninfested trees, which received the same treatment. To our knowledge, no information exists on the relative magnitude of such processes in natural forests. It is likely that the irrigation schedule used in our experiment, like the quantity of precipitation in field situations, is critical for throughfall chemistry. Using actual rainfall, with periods of high and low precipitation, is likely to influence biological processes in the phyllosphere more than applying constant quantities of rain according to annual averages. For example, a long period without rain is known to result in the crystallization of honeydew on Norway spruce (Zoebelein, 1956; Scheurer, 1964), which is likely to be unavailable to micro-organisms. Equally, heavy rain may wash off the carbohydrates, which then become unavailable for micro-organisms in the phyllosphere but available to the soil biota. The prevailing weather conditions are therefore crucial not only for the honeydew–micro-organism interaction but also for throughfall chemistry, as it affects the magnitude of nutrient transformation in the phyllosphere and ultimately the C and N input into the forest floor. In the future, investigations must quantify the transition processes involving herbivores and micro-organisms in different compartments, under different environmental conditions, in order to evaluate their importance relative to leaching or nutrient cycles. The processes described above indicate a very rapid affect of the carbohydrates provided by aphids on inorganic N-compound depletion by the microbes in the phyllosphere. We support the view that a better understanding of biological and ecosystem processes will be achieved more quickly if studies on the effects of organisms on nutrient cycling take into account the ecology of energy providers, such as aphids, and energy consumers, such as micro-organisms (Vitousek, 1990; Grimm, 1995).

Acknowledgements

We wish to thank E. Matzner for critical comments on an earlier draft of the paper. Tony Dixon helped to focus the subject. A. Glaβer, K. Moser, B. Popp and C. Stöcker helped with the chemical analyses. Financial support was given by the German Ministry for Research and Technology (Fördernummer: BMBF No. PT BEO 51-0339476B).

References

Allen, G. (1981) *Laboratory Techniques in Biochemistry and Molecular Biology; Sequencing of Proteins and Peptids*. North Holland, Amsterdam.

Apps, M.J. & Price, D.T. (1996) The global perspective. *Forest Ecosystems, Forest Management and the Global Carbon Cycle* (ed. by M. J. Apps and D. T. Price), pp. 1–15. Springer-Verlag, Berlin.

Asner, G.P., Seastedt, T.R. & Townsend, A.R. (1997) The decoupling of terrestrial carbon and nitrogen cycles. *Bioscience*, **47**, 226–234.

Benedict, J.H., Chang, J.F. & Bird, L.S. (1991) Influence of plant microflora on insect-plant relationships in *Gossypium hirsutum*. *Microbial Mediation of Plant–Herbivore Interactions* (ed. by P. Barbosa, V. A. Krischik and C. G. Jones), pp. 273–307. John Wiley and Sons, Inc., New York.

Brock, T.D. & Madigan, M.T. (1991) *Biology of Microorganisms*, 6th edn. Prentice Hall, Englewood Cliffs, New Jersey.

Carroll, G.C. (1979) Needle microepiphytes in Douglas fir canopy: biomass and distribution patterns. *Cannadian Journal of Botany*, **57**, 1000–1007.

Choudhury, D. (1988) Herbivore induced changes in leaf-litter resource quality: a neglected aspect of herbivory in ecosystem nutrient dynamics. *Oikos*, **51**, 389–393.

Dik, A.J., Fokkema, N.J. & van Pelt, J.A. (1991) Consumption of aphid honeydew, a wheat yield reduction factor, by phyllosphere yeast under field conditions. *Netherland Journal of Plant Pathology*, **97**, 209–232.

Dixon, A.F.G. (1971a) The role of aphids in wood formation. I. The effect of the Sycamore aphid, *Drepanosiphum plantanoides* (Schr.) (Aphididae), on the growth of Sycamore, *Acer pseudoplantanus* (L.). *Journal of Applied Ecology*, **8**, 165–179.

Dixon, A.F.G. (1971b) The role of aphids in wood formation. II. The effect of the Lime aphid, *Eucallipterus tiliae* L. (Aphididae), on the growth of Lime, *Tilia vulgaris* Hayne. *Journal of Applied Ecology*, **8**, 393–399.

Grier, C.C. & Vogt, D.J. (1990) Effects of aphid honeydew on soil nitrogen availability and net primary production in an *Alnus rubra* plantation in Western Washington. *Oikos*, **57**, 114–118.

Grimm, N. (1995) Why link species and ecosystems? A perspective from ecosystem ecology. *Linking Species and Ecosystems* (ed. by C. G. Jones and J. Lawton), pp. 5–15. Chapman & Hall, New York.

Huntly, N. (1991) Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics*, **22**, 477–503.

Huntly, N. (1995) How important are consumer species to ecosystem functioning? *Linking Species and Ecosystems* (ed. by C. G. Jones and J. Lawton), pp. 72–83. Chapman & Hall, London.

James, F.C. & McCulloch, C.E. (1990) Multivariate analysis in ecology and systematics: pancea or Pandora's box? *Annual Review of Ecology and Systematics*, **21**, 129–166.

Jermyn, M.A. (1975) Increasing the sensitivity of the anthrone method for carbohydrate. *Analytical Biochemistry*, **68**, 332–335.

Joergensen, R.G. & Brookes, P.C. (1990) Ninhydrin-reactive nitrogen measurements of microbial biomass in 0.5m K_2SO_4 soil extracts. *Soil Biology and Biochemistry*, **22**, 1023–1027.

Johnson, N.E. (1965) Reduced growth associated with infestations of Douglas-fir seedlings by *Cinara* species (Homoptera: aphidae). *Canadian Journal of Entomology*, **97**, 113–119.

Krischik, V.A. & Jones, C.G. (1991) Micro-organisms: The unseen mediators. *Microbial Mediation of Plant–Herbivore Interactions* (ed. by P. Barbosa, V. A. Krischik and C. G. Jones), pp. 1–6. John Wiley and Sons, Inc., New York.

Llewellyn, M. (1975) The effect of the lime aphid (*Eucallipterus tiliae* L.) on the growth of the lime tree (*Tilia* x *vulgaris* Hayne) II. The primary production of saplings and mature trees, the energy drain imposed by the aphid populations and revised standard deviations of aphid population energy budgets. *Journal of Applied Ecology*, **12**, 15–23.

Manderscheid, B. & Göttlein, A. (1995) Wassereinzugsgebiet Lehstenbach – das BITÖK-Untersuchungsgebiet am Waldstein (Fichtelgebirge, NO-Bayern). *Bayreuther Forum Ökologie*, **18**, 1–84.

Matzner, E. (1988) Der Stoffumsatz zweier Waldökosysteme im Solling. *Bericht Forschung Waldökosysteme/Waldsterben University of Göttingen Reihe A*, **40**, 1–217.

Maurizio, A. (1985) Honigtau-Honigtauhonig. *Waldtracht und Waldhonig in der Imkerei* (ed. by W. J. Kloft and H. Kunkel), pp. 267–295. Ehrenwirth, München.

McDowell, W.H. & Likens, G.E. (1988) Origin, composition, and flux of dissolved organic carbon in the Hubbard Brook valley. *Ecological Monographs*, **58**, 177–195.

Michalzik, B., Dorsch, T. & Matzner, E. (1997) Stability of dissolved organic nitrogen (DON) and mineral nitrogen in bulk precipitation and throughfall. *Zeitschrift für Pflanzenernährung und Bodenkunde*, **160**, 433–434.

Müller, H. (1956) Können Honigtau liefernde Baumläuse (Lachnidae) ihre Wirtspflanzen schädigen? *Zeitschrift für Angewandte Entomologie*, **39**, 168–177.

Ohmart, C.P., Stewart, L.G. & Thomas, J.R. (1983) Leaf consumption by insects in three *Eucalyptus* forest types in southeastern Australia and their role in short-term nutrient cycling. *Oecologia*, **59**, 322–330.

Pastor, J.B., Dewey, R.J., Naiman, F.P. & McInnes. & Cohen, Y. (1993) Moose browsing and soil fertility in the boreal forests of Isle Royale national park. *Ecology*, **74**, 467–480.

Qualls, R.G., Haines, B.L. & Swank, W.T. (1991) Fluxes of dissolved organic nutrients and humic substances in a deciduous forest. *Ecology*, **72**, 254–266.

Romme, W.H., Knight, D.H. & Yavitt, J.B. (1986) Mountain pine beetle outbreaks in the Rocky Mountains: regulators of primary productivity? *American Naturalist*, **127**, 484–494.

Scheurer, S. (1964) Zur Biologie einiger Fichten bewohnender Lachnidenarten (Homoptera, Aphidina). *Zeitschrift für Angewandte Entomologie*, **53**, 153–178.

Schowalter, T.D., Hargrove, W.W. & Crossley, D.A. Jr (1986) Herbivory in forested systems. *Annual Review of Entomology*, **31**, 177–196.

Seastedt, T.R. & Crossley, D.A. Jr (1984) The influence of arthropods on ecosystems. *Bioscience*, **34**, 157–161.

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. (1996) Aphid honeydew and its effect on the phyllosphere microflora of *Picea abies* (L.) Karst. *Oecologia*, **108**, 771–776.

Swank, W.T., Waide, J.B., Crossley, D.A. Jr & Todd, R.L. (1981) Insect defoliation enhances nitrate export from forest systems. *Oecologia*, **51**, 297–299.

Townsend, A.R. & Rastetter, E.B. (1996) Nutrient constraints on carbon storage in forested ecosystems. *Forest Ecosystems, Forest Management and the Global Carbon Cycle* (ed. by M. J. Apps and D. T. Price), pp. 35–45. Springer-Verlag, Berlin.

Tukey, J.W. (1970) The leaching of substances from plants. *Annual Review of Plant Physiology*, **21**, 305–324.

Vitousek, P.M. (1990) Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos*, **57**, 7–13.

Zoebelein, G. (1954) Versuche zur Feststellung des Honigtauertrages von Fichtenbeständen mit Hilfe von Waldameisen. *Zeitschrift für Angewandte Entomologie*, **36**, 358–362.

Zoebelein, G. (1956) Der Honigtau als Nahrung der Insekten. *Zeitschrift für Angewandte Entomologie*, **38**, 369–416.

Zwölfer, W. (1952) Die Waldbienenweide und ihre Nutzung als forstentomologisches Problem. *Verhandlungen der deutschen Gesellschaft für angewandte Entomologie, Frankfurt*, **1952**, 164–168.

Accepted 9 November 1998