Oecologia (1996) 108:771–776

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Aphid honeydew and its effect on the phyllosphere microflora of *Picea abies* (L.) Karst.

Received: 26 April 1996 / Accepted: 12 June 1996

Abstract Aphids of the genus *Cinara*, feeding on Norway spruce, excrete copious amounts of honeydew, a carbon-rich waste product, which accumulates locally on needles and twigs. We investigated the role of honeydew as a potential source of energy which might promote the growth of micro-organisms in the phyllosphere of conifer trees. To approach this question, we followed the population dynamics of *Cinara* spp. in a natural forest stand over two seasons. We also studied the amounts of honeydew produced by individual aphids and identified potential parameters which might influence honeydew production. Finally, we determined the growth of micro-organisms on infested and uninfested needles of Norway spruce during the growing season. Confined to *Picea abies*, the investigated *Cinara* species only became abundant in midsummer, when needles and shoots were expanding. The populations showed only a single peak in abundance, the timing and magnitude of which may vary from year to year due to weather conditions, changes in plant quality in a yearly cycle or the impact of natural enemies. The amount of honeydew produced by individual aphids was dependent on the developmental stage of the aphid, the nutritional supply of its host plant and on the developmental state of the Norway spruce (e.g. bud burst, end of shoot extension). The presence of honeydew significantly increased the growth of bacteria, yeast and filamentous fungi on the surface of needles and there was a pronounced seasonal trend, with the highest abundance in midsummer correlating with the period of peak aphid abundance. Taken together, these findings indicate that aphids have an influence on microbial ecology in the phyllosphere of trees. The implication of our study, from interactions at the population level to effects and potential consequences for C and N fluxes at the level of forest ecosystems, is discussed.

Key words Aphid honeydew · Epiphytic micro-organisms · Conifers · Phyllosphere

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Introduction

In 1976, Owen and Wiegert formulated the hypothesis that insect herbivores such as aphids, which feed on the phloem sap of plants, may increase plant fitness. Their line of argumentation is that aphids produce prodigious amounts of honeydew, an energy-rich food resource. This source of easy accessible carbohydrate could then be used by micro-organisms which might be stimulated to fix higher amounts of nitrogen or mobilise soil nutrients, which then become available to the infested plant. Although this hypothesis is tempting it has received considerable criticism, especially the claim for mutualistic interactions between herbivores and their host plants. Several studies have tested this hypothesis; however, most were confined to the laboratory. Petelle (1980) demonstrated that there is some possibility of enhanced nitrogen fixation in soil micro-organisms when individual sugars are added to the soil. In addition, the biomass of fungi was shown to increase by 30% and that of bacteria by 300% (Dighton 1978). However, far more evidence indicates that aphids exert a severe nutrient drain on their host plants, which respond with reduced seed production (Choudhury 1984; Foster 1984) or reduced biomass accumulation (Johnson 1965; Dixon 1971a, b; Stadler 1996). Nevertheless, surprisingly little information is available on the processes associated with the production and accumulation of honeydew in the phyllosphere, especially its effect on the growth of micro-organisms. In this study we report on the honeydew production of the aphid species *Cinara pruinosa* (Hartig) and *Cinara pilicornis* (Hartig) which live exclusively on Norway spruce [*Picea abies* (L.) Karst.] and examine their influence on the growth of micro-organisms on needles during the vegetation period. Both aphid species are

classified as major sources of honeydew in forest ecosystems (Kunkel and Kloft 1985). Honeydew, a waste product of the aphid mode of feeding, has received considerable attention, in economic terms, from the bee-keeping and timber production industries, but its effect on micro-organisms or ecosystem processes has been so far rather neglected.

In particular, we address the following questions: (1) Is there a phenological relationship between the abundance of aphids and micro-organisms? That is, do the population dynamics of aphids correspond to the growth and abundance of micro-organisms on needles of infested twigs? (2) Which parameters influence the production of honeydew? (3) What types of micro-organisms (if any) are promoted in their growth if honeydew is available as an energy-rich resource on infested trees? (4) Are there micro-organisms in the phyllosphere which are able to metabolise ammonia or nitrate, two types of N source which are readily available on needles from atmospheric deposition? (Schulze et al. 1989; Pearson and Stewart 1993).

We discuss our findings with respect to the seasonal dynamics in plant-aphid interactions and consider the possible consequences for the plant-aphid-micro-organism food chain. We also consider the effects of aphid population dynamics, via honeydew, on the abundance of micro-organisms and the possible influences on the carbon and nitrogen balance of forest ecosystems. In doing so, we stress the importance of integrating population ecology and ecosystem analysis to better understand the dynamics of many natural processes.

Materials and methods

Seasonal abundance of *Cinara* species on Norway spruce

Our investigation site is located in the Fichtelgebirge in north-eastern Bavaria in the Waldstein watershed, 800 m above sealevel. The spruce trees were 10–15 years old and exposed to the south-west. In 1994 and 1995, we surveyed aphid numbers at 2-week intervals from April until October to follow the population dynamics of the Lachnids. Knowledge of the periods of low and peak aphid abundance in 1994 was considered necessary to set the timing of sample collection for the microbiological analyses in the phyllosphere in the following year. At each sampling date, the number of infested trees was determined plus their number of infested twigs. In addition, we counted the number of aphids on each infested twig encountered randomly within 2 h of searching.

Amount of honeydew produced on Norway spruce under laboratory conditions

To investigate the influence of host plant quality on the honeydew production of *C. pruinosa* and *C. pilicornis,* we planted ten 3-year-old seedlings of *P. abies* in pots filled with either high-quality compost soil or with sand containing no nutrients. The latter treatment was chosen to obtain host plants of poor quality with yellowing needles. Needle yellowing is a widespread symptom of many Spruce trees in the Fichtelgebirge area. The resulting two extremes of plant quality were expected to represent the limits of the range of plant qualities *Cinara* species will encounter and to which they have to adapt in terms of food uptake and honeydew production in a natural forest stand. In addition, the experiments began at bud burst and lasted until shoot growth ceased, to follow the intrinsic lifecycle of a tree, which we also expected to affect honeydew production. We investigated honeydew production of four different larval instars (L1–L4) and adult aphids. The experiments were started by transferring a single newborn aphid to a *P. abies* shoot. The next day, a small piece of preweighed aluminium foil was clipped underneath each aphid to collect the honeydew excreted. After 24 h, the foils were replaced and the development of the aphids recorded. All foils with the collected honeydew were then dried at 40°C for 48 h and reweighed on a Sartorius microbalance (sensitivity 1 μg). In this way, honeydew production was followed during the complete development of an aphid and for two aphid generations. The experiments started with *C. pruinosa* because this species prefers to feed on 2- to 3-year-old shoots. After bud burst, *C. pilicornis* individuals were added because this species prefers to feed on the newly developing shoots. A total of 101 *C. pruinosa* and 44 *C. pilicornis* individuals were tested. The temperature was set to 22 ± 1°C, 65% relative humidity and 5000 lux light intensity.

Growth of mircro-organisms on infested and uninfested needles of Norway spruce

In 1995 we collected 1- and 2-year-old shoots from Norway spruce infested with *Cinara* spp. and from uninfested controls on three sampling dates. The first sample was taken at the end of May (29 May) when aphid population densities were still low. The second sample was taken during the peak densities at the beginning of July (3 July) and the last sample was collected at the beginning of September (5 September) when aphid numbers became low again, mainly as a result of heavy destruction of their colonies by natural enemies. Our sampling dates were also influenced by the weather conditions, because we only chose sample dates prior to which at least 1 week without precipitation was recorded, to allow honeydew accumulation in the phyllosphere.

Microbiological analyses

Needles of *P. abies* were cut off from the twigs with sterile scissors. From each sample, 25 g was blended in 225 ml sterile distilled water in a Stomacher lab blender for 2 min. Immediately after blending, the samples were logarithmically diluted in quarter-strength Ringer's solution and analysed by spread plating. Total aerobic, heterotrophic bacteria populations were enumerated on Standard II nutrient agar (Merck) (complete medium). To detect those bacteria which were able to utilise ammonia or nitrate as a nitrogen source, the samples were spread on the following mineral medium (l^{-1}): NH_4Cl (medium 2) or $NaNO_3$ (medium 3) 1.5 g, glucose 5 g, KH_2PO_4 0.4 g, K_2HPO_4 0.1 g, $MgSO_4 . 7H_2O$ 0.2 g, NaCl 0.1 g, $FeCl_3$ 10 mg, $Na_2MoO_4 . 2H_2O$ 2 mg, yeast extract (Merck) 50 mg, solution of trace elements (Drews 1983) 1.0 ml and agar 15 g. All media for the detection of bacteria were supplemented with 0.4 g/l cycloheximide (Merck) to inhibit the growth of fungi. The pH of these media was adjusted to 6.5.

Sabouraud-1% dextrose-1% maltose agar (Merck) was used to enumerate total yeast and filamentous fungi, which were easily distinguished on the basis of their colony forms. Fungi, able to utilise inorganic nitrogen sources, were detected on the following mineral medium (l^{-1}): NH_4Cl (medium 2) or $NaNO_3$ (medium 3) 1.5 g, glucose 10 g, maltose 10 g, yeast extract (Merck) 50 mg, solution of trace elements (Drews 1983) 1.0 ml and agar 15 g. Chloramphenicol (Berlin-Chemie) was added at 0.4 g/l to suppress bacterial growth. The fungi media were adjusted to a pH of 5.5. All media plates were incubated at 25°C for 5 days.

Results

Aphid abundance is shown in Fig. 1A for biweekly intervals in terms of proportions of trees infested and proportions of twigs infested per tree. In 1994, roughly 30% of

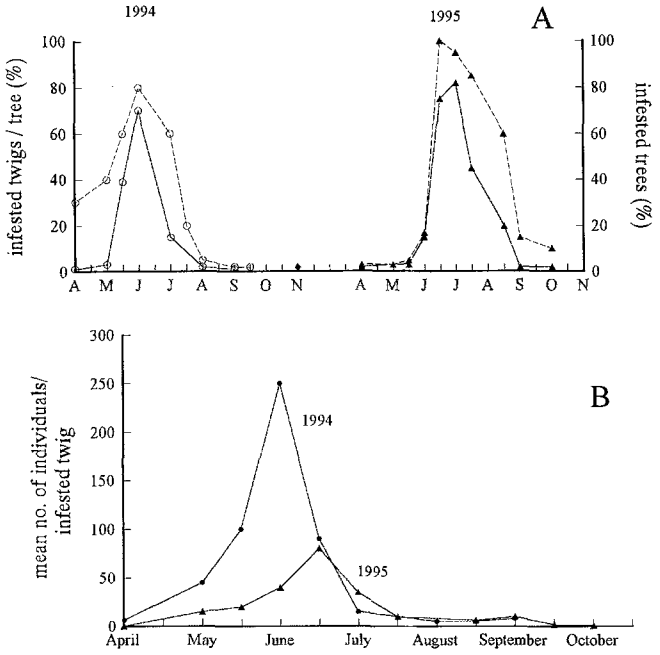

Fig. 1 **A** Mean relative numbers of trees infested with *Cinara* spp. (*dashed line*) and infested twigs/tree (*solid line*) at the Waldstein site from April until November in 1994 and 1995. **B** Phenology of *Cinara* spp. on Norway spruce from April until October 1994 and 1995 at the Waldstein site

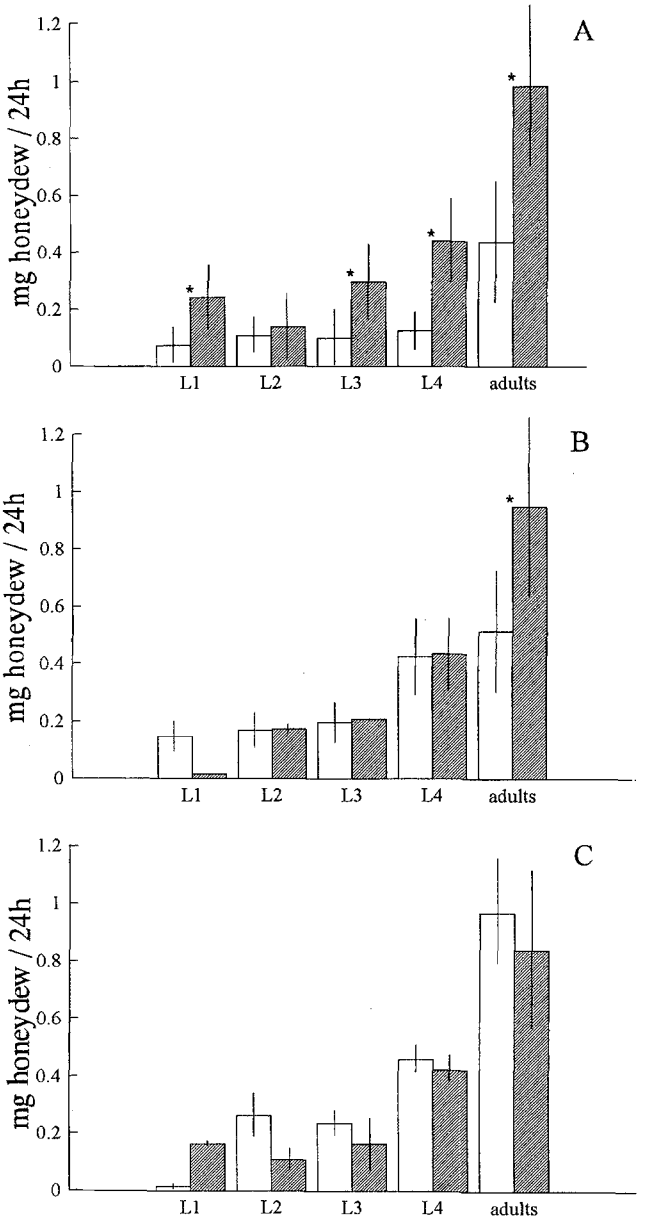

Fig. 2A–C Dry mass of honeydew production of *C. pruinosa* and *C. pilicornis* on seedlings of Norway spruce within 24 h. *L1–L4* indicate the four larval instars of the aphid species. *Vertical lines* give the SD of the means. Pairs of columns marked with an *asterisk* differ significantly at $P<0.05$ (Mann-Whitney U statistic). □ High-quality treatment, ▨ low-quality treatment. **A** Honeydew production of *C. pruinosa* at bud burst. **B** Honeydew production of *C. pruinosa* at the end of the shoot extension phase. **C** Honeydew production of *C. pilicornis* at the end of the shoot extension phase

all trees were infested in the spring, which is primarily due to high numbers of overwintering eggs. Following rapid multiplication, the aphids had infested more than 80% of the trees by mid June. However, a heavy decline in aphid numbers followed, mainly due to the strong impact of natural enemies such as coccinellids, syrphids and spiders. In mid August, only a few trees were still infested. A similar picture evolved in 1995. However, the number of infested trees was low until the beginning of June, most likely as a result of low egg densities on needles at the end of the previous year. From the middle of June, many alates were recolonising the trees at this site resulting in a 100% infestation rate. The decline in the number of trees infested from July onwards is again attributable to colony destruction by natural enemies.

The number of infested twigs per infested tree roughly followed the overall scheme for tree infestation, with a maximum of 80% of all twigs infested in June 1994 and July 1995. This can be ascribed to two processes. First, the intrinsic tendency of individual aphids to spread within a host tree and second, to the immigration of alate morphs.

Comparing the trends in the mean number of individuals on infested twigs for 1994 and 1995, deviations in the size of aphid colonies were substantial (Fig. 1B). In 1994, a mean of 250 individuals formed dense clusters of colonies in mid June on the twigs of Norway spruce with huge amounts of honeydew crystallising on the surface of needles. In 1995, aphid numbers peaked at the beginning of July with a mean of only 70 individuals per colony. However, aphids were not evenly distributed on their host trees. Some trees were heavily infested, becoming "hot spots" from which neighbouring trees could become colonised. On most twigs, only colonies comprising 5–20 individuals persisted. Many colonies were repeatedly destroyed but twigs were also frequently recolonised.

To quantify the importance honeydew production for a forest ecosystem, it is necessary to investigate the amounts produced by individual species or morphs. Figure 2A–C shows the dry mass of honeydew produced

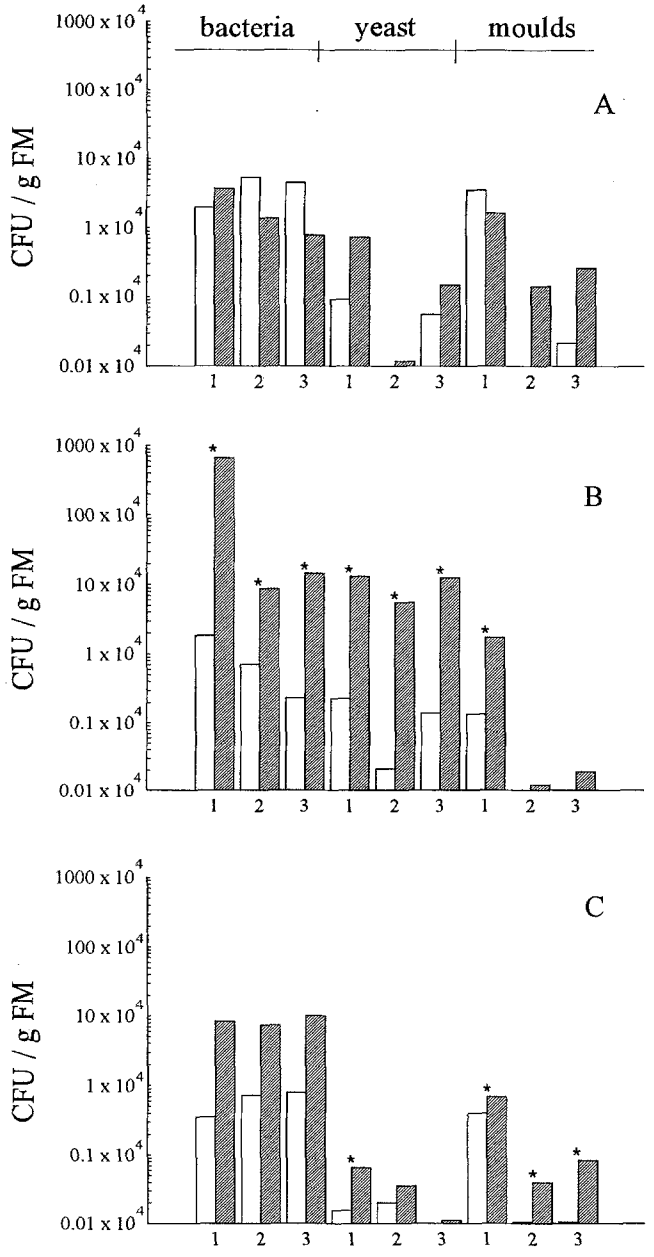

Fig. 3A–C Number of colony-forming units (*CFU*) of aerobic, heterotrophic bacteria, yeast and filamentous fungi per gram needle fresh mass (*FM*) of twigs sampled from Norway spruce either uninfested (□) or infested (▨) with *Cinara* spp. Pairs of columns marked with an *asterisk* differ significantly at $P<0.05$ (Mann-Whitney *U* statistic). 1, complete medium; 2, mineral medium with NH_4^+; 3, mineral medium with NO_3^-. Sample dates in 1995: **A** 29 May, **B** 3 July, **C** 5 September

within 24 h for different treatments, morphs and species. Two results are important. First, the amount of honeydew produced increased from the first-instar larvae to the adult aphids, which might be associated with an increase in body mass and second, aphids feeding on low-quality plants often produced significantly more honeydew than their siblings on high-quality plants (Fig. 2A). However, these differences were smaller when needle and shoot growth had ceased (Fig. 2B): the amount of honeydew produced by aphids feeding on plants from the high-quality treatment then approached that of aphids feeding on plants from the low-quality treatment. The high standard deviations might be attributable to several sources of error such as our inability to control physiological changes prior to when the aphids begin to cast off their exuviae (during which, honeydew production stops for several hours), leaving the feeding site for some time during night hours, local differences in shoot quality, or droplets of honeydew dislodged on needles and thus not collected on the aluminium foil. *C. pilicornis* individuals, which prefer to feed on developing shoots, also showed no differences in the amounts of honeydew produced due to the different nutrient regimes of their host plants at the end of the shoot extension period (Fig. 2C).

Figure 3 shows that all types of micro-organism investigated on Norway spruce needles often increased in numbers when aphid honeydew was available. The highest cell densities were achieved in midsummer (Fig. 3B), when the aphids reached their maximum densities (Fig. 1A) and high rates of honeydew production. Above all, some fungi which were able to utilise inorganic nitrogen increased on needles infested with aphids. At the end of May, while the *Cinara* populations were still growing, bacteria, yeast and moulds remained unaffected, as the treatment groups did not differ significantly (Fig. 3A). The cell counts for the late samples (Fig. 3C) indicated a still favourable effect of honeydew on the microbial epiphytes although the aphid populations had already broken down.

Discussion

Owen and Wiegert's (1976) hypothesis of mutualistic interactions between aphids and their host plants has attracted much criticism (Foster 1984; Choudhury 1985) but also inspired several experiments to evaluate its implications for plant fitness. Most studies, however, concentrated on the effects of aphid honeydew on soil nitrogen availability (Choudhury 1984; Grier and Vogt 1990) but neglected possible effects on micro-organism growth in the phyllosphere. Only some 2–3% of the honeydew produced by aphids on trees is considered to reach the soil directly (Choudhury 1985), making direct interactions between honeydew and soil micro-organisms unlikely. Instead, much of the honeydew produced is consumed by other insects. For example, Zoebelein (1956) lists more than 250 insect species which at least temporarily consume aphid honeydew and tending ants alone may consume more than two-thirds of the honeydew available (Müller 1956, 1960). However, literature surveys on ant tending showed that only a quarter to one-third of all aphid species are obligatory myrmecophiles (Bristow 1991; Stadler 1996). In central Europe, five species of the genus *Cinara* are known to feed on Norway spruce. Two of them are obligate myrmecophiles, one is facultative and the last two species are classified as non-myrmecophiles (Scheurer 1964; Kunkel and

Kloft 1985; Blackman and Eastop 1994). Therefore, considerable amounts of honeydew might be available for micro-organisms in the phyllosphere of Norway spruce.

The abundance of *Cinara* species typically shows a single peak in mid summer (Fig. 1A) with huge amounts of honeydew accumulating on needles and shoots at that time. Honeydew production is influenced by several parameters such as the developmental stage of the aphid instar, the developmental stage of the host plant and its nutritional supply (Fig. 2A–C). Aphids feeding on poor-quality hosts with yellowing needles and on hosts which have ceased shoot elongation produce significantly more honeydew than aphids on well-nourished plants at the time of bud burst. Therefore, it is reasonable to suspect that honeydew production and its availability in the field is a site-specific and time-dependent process influenced by weather and soil conditions. The amounts of honeydew produced on conifers, published for different *Cinara* species, range between 400–700 kg fresh mass/hectare per year (Zwölfer 1952; Zoebelein 1954; Eckloff 1972) and it consists of several sugars of which fructose, saccharose and melezitose comprise more than 90% of the total dry mass (for an overview see Maurizio 1985). This energy-rich source is metabolised by several micro-organism species. However, the population dynamics of aphids indicate that honeydew is not a source which is evenly distributed in the habitat but is concentrated on a few trees which mark "hot spots". This is particularly so in springtime before alate dispersion. Reports on high variability in nitrogen or carbon concentrations collected from throughfall in natural forest stands might originate in the population dynamics of associated aphid species.

Nutrients enhancing microbial growth in the phylloplane may originate from several sources such as soil particles, dust, pollen, ions, solutes in rainwater, dead micro-organisms or insect excrement (Dik 1991; Andrews 1992). On lime trees, a drain of 2–50 kg dry mass/tree per year was reported through the excretion of honeydew by *Eucallipterus tiliae* (L.) (Heimbach 1986), which could become equivalent to the net annual primary production of these trees (Llewellyn 1975). The effect of honeydew on the growth of yeast populations is well-known, especially for deciduous trees such as sycamore (Rodger and Blakeman 1984) but also on wheat (Dik et al. 1991). However, its contribution to ecological or ecosystem processes such as C/N fluxes is difficult to determine. Studies in deciduous forests have shown that total N fluxes in throughfall may reach 30–40 kg/hectare per year (Matzner 1988). About one-third of the C and up to one-half of the dissolved N from throughfall is organic (Matzner 1988; Qualls et al. 1991) and its origin is usually ascribed to foliar leaching. However, interactions between aphid honeydew, microbial growth and secondary biotic processes in the phyllosphere have not been considered in this respect up to now.

Micro-organisms are usually described as aggregating in the midribs along the upper surface of needles (Bernstein and Carroll 1977; Canny 1990) and they seem to grow better in the lower canopy or shaded strata where highest humidities are recorded (Andrews 1992). Carroll (1979) reported the total volume of microbial cells on the needles of a single Douglas fir to be as high as 1093 cm^3, which would yield a biomass of 38–60 kg/tree. However, considering the stochastic nature of many spatial and temporal interactions between many organisms (e.g. temperature, humidity, natural enemies), we are still far from being able to quantify microbial production or aphid biomass/honeydew accumulation on a larger scale.

Dik and Pelt (1993) showed that honeydew on wheat leaves can stimulate the growth of pathogenic filamentous fungi, while bacteria remained unaffected by this source of energy. As in earlier investigations on sycamore leaves by Rodger and Blakeman (1984), these authors demonstrated that aphid honeydew is mainly consumed by saprophytic yeast which could apparently prevent the accumulation of honeydew in the phyllosphere. However, there was no indication of a direct effect of honeydew on the increase in the yeast population. This is in contrast to our study, where the growth of moulds, yeast and bacteria was found to be stimulated by aphid honeydew. The difference might be due to the state of nutrients available to micro-organisms in the phyllosphere of Norway spruce, which is probably very poor in nutrients. This suggestion is supported by the fact that bacteria with fastidious nutritional requirements, such as enterobacteria or lactic acid bacteria, could not be detected on the needles after an enrichment procedure (unpublished data). Hence, a supplement of energy in the form of honeydew into this habitat could have a more pronounced effect on the epiphytic microflora than on leaves of deciduous trees or Gramineae, whose exudates usually provide a better nutritional source for microbial epiphytes (Tukey and Tukey 1969).

The density of epiphytic micro-organisms seems to be limited by the low availability of carbon in the phyllosphere. Therefore, if honeydew is available, micro-organism growth is promoted. This is also true for those micro-organisms able to grow with ammonia or nitrate as the sole N source, possibly originating from deposition. The biomass and metabolic activity of these micro-organisms could be a source of organic N in forest ecosystems. Our findings corroborate the suggestion that most bacteria are able to utilise ammonia (Brock and Madigan 1991) as well as nitrate (Campbell 1977; Schlegel 1992). We demonstrated that most yeasts also have this ability. However, in filamentous fungi, the ability to metabolise honeydew varies considerably and we need further investigations aimed at identifying those micro-organisms amongst the epiphytes on spruce needles able to utilise inorganic N sources and quantifying their N metabolism.

Integrating species and ecosystem ecology has often been found difficult because different questions are addressed. One major distinction is a focus on organisms versus a focus on materials and energy fluxes (Pickett et al. 1994). However, we have no doubt that if we are to understand vital ecosystem processes or fluxes (C and N cycles) across different levels of organisation (Schulze

and Zwölfer 1994), it appears necessary that we identify interactions between different trophic levels, e.g. analysing sources of variation in aphid abundance, honeydew production and micro-organism growth in the phyllosphere. Aphids, which excrete large amounts of honeydew, affect the growth of bacteria, yeast and fungi. Therefore, knowledge on aphid population fluctuations is likely to promote our understanding of the ecology of microorganisms and contribute to our understanding of ecosystem dynamics and to our identification of the potential contributors to the C and N budgets of ecosystems.

Acknowledgements We wish to express our gratitude to E. Matzner and W. Seyfarth for critical comments on earlier drafts of our manuscript. We also wish to thank Liane Lingk for her excellent technical assistance in microbiological analyses. Financial support was given by the German Ministry for Research and Technology (Fördernummer: BMBF no. PT BEO 51-0339476B).

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