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Resource dynamics in an early-successional plant community are influenced by insect exclusion

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Abstract

The exclusion of insects from terrestrial ecosystems may change productivity, diversity and composition of plant communities and thereby nutrient dynamics. In an early-successional plant community we reduced densities of above- and below-ground insects in a factorial design using insecticides. Beside measuring vegetation dynamics we investigated the effects of insect exclusion on above- and below-ground plant biomass, below-ground C and N storage by plants, litter quality, decomposition rate, soil water content, soil C:N ratio, nutrient availability and soil microbial activity and biomass.

The application of soil insecticide had only minor effects on above- and below-ground biomass of the plant community but increased carbon content in root biomass and total carbon and nitrogen storage in roots. In one of the three investigated plant species (*Cirsium arvense*), application of soil insecticide decreased nitrogen concentration of leaves (−12%). Since *C. arvense* responded positively to soil insecticide application, this effect may be due to drought stress caused by root herbivory. Decomposition rate was slightly increased by the application of above-ground insecticide, possibly due to an impact on epigeic predators. The application of soil insecticide caused a slightly increased availability of soil water and an increased availability of mineralised nitrogen (+30%) in the second season. We explain these effects by phenological differences between the plant communities, which developed on the experimental plots. Microbial biomass and activity were not influenced by insecticide application, but were correlated to above-ground plant biomass of the previous year. Overall, we conclude that the particular traits of the involved plant species, e.g. their phenology, are the key to understand the resource dynamics in the soil.

Keywords: Insecticides; Insect herbivores; Nutrient cycling; Soil insects; Trophic interactions; Vegetation dynamics

1. Introduction

Herbivores influence the composition and structure of plant communities and therefore the trajectories and rates of succession (Crawley, 1997). The impact of herbivorous invertebrates is supposed to be low when compared with grazing and browsing by vertebrates (Crawley, 1989). Nevertheless, it has been repeatedly shown that insect herbivory may play an important role during early succession (Shure, 1971; Gibson et al., 1987; Brown and Gange, 1992; Bach, 1994; Carson and Root, 1999, 2000; Schädler et al., 2004).

The influence of herbivory extends beyond direct effects on plant fitness and competitive relationships between plant species. Firstly, herbivores can influence biomass, composition and diversity of plant communities which in turn affects nutrient dynamics of the ecosystem (Hobbie, 1992; Hooper and Vitousek, 1998; Wardle et al., 2000). Herbivores prefer fast growing plant species with high contents of nutrients and low contents of carbon based defence traits (e.g. secondary compounds, lignin, cellulose). These traits also control the decomposition of litter resulting in a positive correlation between plant palatability and litter decomposability (Grime et al., 1996; Schädler et al., 2003b).

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By decreasing the abundance of palatable plants, herbivores may shift the composition of a plant community toward less palatable and at the same time less degradable plants (Ritchie et al., 1998; Wardle et al., 2002; but see Schädler et al., 2003b). Secondly, plants can respond to herbivory by increasing secondary compounds in the tissue, which decrease decomposition rates of the litter (Bardgett et al., 1998). This in turn has an effect on nutrient cycling, because more nutrients become fixed in the detritus. On the other hand, by increasing root exudation of carbohydrates, herbivory may stimulate the activity of soil microflora and therefore accelerate nutrient cycling (Bardgett et al., 1998). It is, however, far from clear whether these mechanisms are important for plant communities in natural systems.

Overall, the changes in structure and dynamics of plant communities triggered by herbivores will influence the resource use of vegetation and the turnover of organic matter. Even though we have some information about the effects of vertebrate grazers on nutrient cycling (e.g. Frank et al., 2000), much less information is available on the possible role of herbivorous invertebrates. Brown (1994) and Brunsting and Heil (1985) showed that insect herbivores decreased plant biomass and thereby increased availability of nutrients in the soil. In a recent study, Uriarte (2000) demonstrated that in the short term excluding insects from a *Solidago altissima* stand resulted in a decrease of nutrient availability due to a higher plant biomass. In the longer run (17 years), however, insect herbivory decreased litter quality and nutrient levels in the soil. Here, we report the results of an insect exclusion experiment on a set-aside field to evaluate the effects of insect exclusion by insecticides on the resource dynamics during the early stage of secondary succession on a set-aside field.

2. Materials and methods

2.1. Study site

In 1998, we established a field experiment in Central Germany (Bad Lauchstädt near Halle, Saxony-Anhalt, Germany 110 m NN), an area of low annual rainfall (480 mm) and a mean annual temperature of 8.8 °C. The soil is a Chernosem with high nutrient levels (mean across all experimental plots: C-content 1.89%, N-content 0.16%, NO_3^- 1.09 mg/100 g soil, NH_4^+ 0.03 mg/100 g soil, $P_2O_4^{3-}$ 46.8 mg/kg soil). The experimental site is a former arable field with barley the last crop in 1997. The field was ploughed and harrowed in winter 1997 and subsequently the vegetation developed from the seed bank and root fragments. In the first year, the plant community was dominated by monocarpic forbs (e.g. *Chenopodium album*, *Fallopia convolvulus*). Species germinating in autumn (e.g. *Conyza canadensis*, *Lactuca serriola*) became more frequent during the second season. The only abundant polycarpic species during the first season was *Cirsium arvense*, which developed predominantly from root fragments. In the second year, the two polycarpic clonal herbs *C. arvense* and *Epilobium adnatum* dominated the communities. During the first year, we measured an above-ground plant biomass of 1056 g m^{-2} in the herbivore-free treatment, which shows the high productivity of our experimental field (for comparison with other studies see Schädler et al., 2003a).

2.2. Insect exclusion experiment

The experiment was arranged in a randomised block design using 12 blocks each with eight plots of 3×3 m. Plots and blocks are separated by 2 m wide walkways from each other and by a 5–10 m wide strip of undisturbed vegetation from the surrounding agricultural fields. We manipulated the densities of above-ground insects and below-ground insects in a factorial design. The density of above-ground insects was reduced by spraying a solution of Perfekthion every 14 days (BASF, dimethoate 40%; 0.36–0.54 ml diluted in 130–170 ml water). The concentration was increased during the vegetation period to keep up with plant growth. Density of below-ground insects was reduced by watering the plots with 1 l suspension of Hortex every 4 weeks (Celaflor, chlorpyrifos 2%; 45 g l^{-1}). In a greenhouse experiment, we found no side effects of the insecticides on two abundant plant species (*C. album*, *F. convolvulus*; Schädler et al., 2004, see also Brown and Gange, 1989; Fraser and Grime, 1997). Furthermore, we are not aware of side effects of these compounds on microflora, vertebrates and non-arthropod invertebrates (see Schädler et al., 2004, for review and for effectiveness of both compounds). Further, in an assessment of the effects of insecticide application on soil animals we found that the application of soil insecticide caused a substantial decrease of densities of all investigated insect taxa, including destruents like springtails and macroinvertebrate predators like staphylinid beetles (Endlweber, unpublished, Alphei, unpublished). However, earthworms and mites in soil were unaffected by the application of insecticides (Endlweber and Scheu, unpublished). Similarly, Edwards and Thompson (1973) found only weak effects of organophosphorus insecticides on mite populations. The insecticides used are therefore considered appropriate for insect exclusion experiments. Controls were treated with water only. In an additional treatment, we applied the molluscicide to half of the plots. Because molluscs were absent on the experimental field in the first years of succession and the molluscicide did not show any effects on vegetation, we excluded the molluscicide treatment from the analysis, which increases the power of the statistical analysis (see Schädler et al., 2004).

2.3. Measurement of vegetation

In August of 1998 and in July of 1999, we measured above-ground biomass on 0.25 m^2 quadrates in five blocks

($n=40$). Vegetation was clipped at the soil surface and dried at 50 °C to weight constancy. From each of these 0.25 m^2 quadrates we removed three randomly placed soil cores (diameter 6 cm; depth 20 cm) and pooled them to a single sample. We washed the soil through a 2 mm sieve. Roots were dried at 50 °C to weight constancy, weighed and ground in a mill. We determined C and N content of roots by using an Elementar Vario EL element analyser (Elementar Analysengeräte GmbH, Hanau, Germany).

Additionally, we assessed the development of vegetation using the point quadrate method eight times a year from April to October in 1998 and 1999. A sampling frame of 1 m^2, divided in 7×7 quadrates, was placed into the centre of the experimental plots. Each of the 49 pins (diameter 3 mm) was placed randomly within one of these quadrates (stratified random sampling, Greig-Smith, 1983). For every plant species, the number of touches of the pins with a living plant was recorded. A detailed outline of the community dynamics can be found in Schädler et al. (2004). In short, insecticide application had only minor effects on total cover abundance and species richness. The application of soil insecticide, however, changed the dominance structure of the plant community in the second year. The Creeping thistle, *C. arvense* was the dominant plant in plots where soil insecticide was applied whereas the Square-stemmed willow herb, *E. adnatum*, was the dominant species on all other plots. In this paper, we refer to these data only for comparison with nutrient dynamics.

2.4. Decomposition

As a substrate to quantify decomposition rate we used leaves of *C. arvense* because it occurred on all experimental plots. Fully expanded leaves of *C. arvense* were collected at the beginning of June 1999 outside the experimental plots and dried at 60 °C to weight constancy. Forty-eight replicates of 1.0 ± 0.1 g were weighed, slightly moistened with deionised water to avoid breakage and sealed within flat litter bags made of polyester (mesh size 1.55 mm). The inner compartment of the litter bags was about 12×8 cm^2. We examined decomposition within the four treatments (control, foliar insecticide, soil insecticide and both compounds). Litter bags were placed in the inner square metre of the experimental plots immediately on the soil surface. During the subsequent insecticide applications care was taken not to contaminate litter bags with the insecticide directly. Litter bags were retrieved after 8 weeks, dried to weight constancy at 60 °C, cleaned and weighed. We defined decomposition rate as the percentage dry mass loss.

2.5. Litter quality

Three plant species were common enough in our experimental plots to allow for the analysis of litter quality (*C. arvense*, *L. serriola*, *E. adnatum*). In September 1999, we sampled about 1 g litter of every plant species on the experimental plots within six blocks ($n=48$ for each species). Freshly senesced litter was collected directly from two to five plants per plot and pooled. We cleaned the litter by gentle brushing. Subsequently the litter was dried at 60 °C to weight constancy and ground in a mill. Three subsamples per plot and species were analysed for C and N content again using an Elementar Vario EL element analyser. Values of the subsamples were averaged.

2.6. Soil analyses

Soil samples were taken prior to the first application of insecticides in March 1998 and subsequently in June 1999 and in August 1999 on all experimental plots. The two latter dates refer to the peak of plant biomass and the time after the first vegetation dieback. Soil samples were taken 4–7 days after rainfall. We took soil cores from three random points in each plot (diameter 2 cm diameter, depth 20 cm) and pooled them. Stones and roots were removed. Samples were sealed in polyethylene bags and stored at −20 °C for subsequent analyses.

For chemical analyses, 50 g of soil were sieved (2 mm). Contents of nitrate (NO_3^-) and ammonium (NH_4^+) were determined colorimetrically after extraction in a 0.0125 M $CaCl_2$-solution (Grimshaw et al., 1989). Total available nitrogen was defined as the sum of nitrate and ammonium. The remaining soil was dried at 60 °C to weight constancy and ground in a mill. Contents of available phosphorus and potassium were determined by inductively coupled plasma atomic emissions spectrometry after extraction in a solution of $C_6H_{12}CaO_6$. Total C and N content were measured using an element analyser. Soil water was determined gravimetrically after drying a subsample of soil at 60 °C to weight constancy.

Soil microflora was analysed at the beginning of the third year of succession (1999) at two dates: before the first insecticide application in March and after two-fold application of soil insecticide and three-fold application of the foliar insecticide in May. We took three soil cores (diameter 5 cm) from each plot. We divided each core into two horizons (0–3 cm, 3–6 cm). For each plot, the three samples of each horizon were pooled. After removing roots and macrofauna by hand, the soil samples were sieved (4 mm). Samples were stored in polyethylene bags at 5 °C. Prior to the respiration measurements the samples were conditioned at room temperature in the dark for 3 days. Respiration was measured by an automated respirometer based on electrolytic O_2-microcompensation (Scheu, 1992). Basal respiration was measured in fresh soil samples equivalent to 4 g dry wt (mean O_2 consumption rates between 10 and 20 h). Microbial biomass was calculated from the maximum initial respiratory response (MIRR [$\mu l\ O_2\ h^{-1}$]; mean of 3–5 h) using the substrate-induced respiration (SIR) method (Anderson and Domsch, 1978) on the same soil samples. Microbial biomass was calculated as $38\times$MIRR (Anderson and Domsch, 1978; Beck et al., 1997) from oxygen consumption of samples supplemented

with 8000 μg glucose g^{-1} dry wt assuming a respiratory quotient of 1 (Ross, 1980). Glucose was added as solution to increase the water content of the samples to the maximum water-holding capacity.

2.7. Data analysis

Prior to statistical analyses, decomposition rates and percentage contents of water, C and N were arcsin-transformed to reduce heterogeneity of variances and non-normality. Values for plant biomass and contents of available nutrients were log-transformed, whereas raw data for C/N-ratios were used.

The effect of insecticide application on decomposition was tested by a two-way ANCOVA (Proc GLM in SAS 8.0). In addition to initial dry mass of leaves, we included total cover abundance as a second covariate in our analyses (square-rooted values of July), because the insecticide application changed vegetation structure and thereby also temperature and moisture. Treatment effects on litter quality were tested for each plant species by two-factorial ANOVA. The influence of insecticide application on soil nutrients, water, C and N was tested in a two-factorial repeated-measures ANOVA (Proc GLM in SAS 8.0). Initial contents in March 1998 (not examined for soil water) were treated as covariates, therefore treatment effects were tested for differences to the start of the experiment.

The metabolic quotient of the soil microflora (qCO_2) was calculated as the ratio of basal respiration to SIR. Effects of insecticide applications and horizon on basal respiration, SIR and qCO_2 were tested by means of three-way repeated-measures ANOVA. For all analyses, block effect was considered as an additional fixed factor and interactions with block were pooled in the error term (see Newman et al., 1997).

3. Results

3.1. Above-ground vegetation and storage of C and N in litter and roots

In the first year of succession, the application of both insecticides tended to increase above-ground biomass (control: 539 ± 71 g m^{-2}, foliar insecticide: 722 ± 104 g m^{-2}, soil insecticide: 803 ± 126 g m^{-2}, both compounds: 1026 ± 189 g m^{-2}; means ± standard error). In the second year, above-ground biomass tended to be higher on plots where we applied the foliar insecticide (control: 530 ± 129 g m^{-2}, foliar insecticide: 720 ± 97 g m^{-2}, soil insecticide: 536 ± 95 g m^{-2}, both compounds: 660 ± 134 g m^{-2}; means ± standard error). However, treatment effects and interactions were not significant ($P > 0.1$). We found a marginally significant increase in root biomass when soil insecticide was applied (ANOVA, $F_{1,32} = 3.06$, $P = 0.09$; control: 164 ± 40 g m^{-2}, foliar insecticide: 142 ± 27 g m^{-2}, soil insecticide: 181 ± 30 g m^{-2}, both compounds: 229 ± 43 g m^{-2}; means ± standard error). As a result, shoot/root-ratio was significantly lower on plots treated with soil insecticide ($F_{1,32} = 4.55$, $P = 0.04$). Content of C in roots showed an increase with the application of soil insecticide (Fig. 1). The application of soil insecticide tended to increase

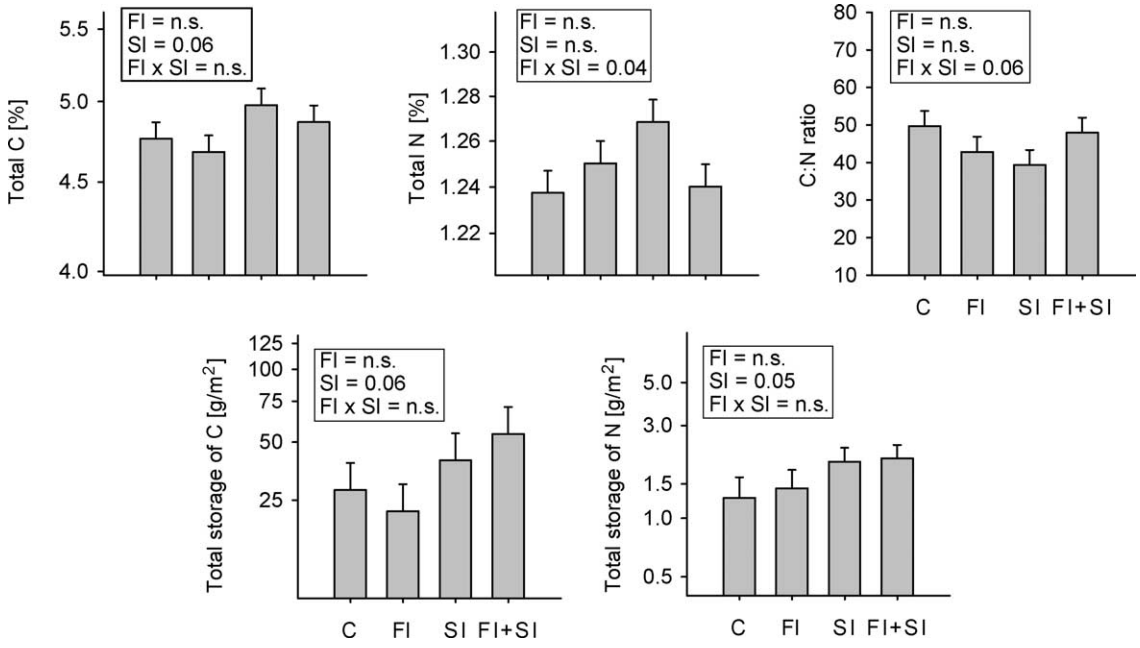

Fig. 1. Effects of insecticide application on concentration and total storage of carbon and nitrogen in roots on the experimental plots (means ± standard error). Note that *y*-axes for total nitrogen and carbon are arcsin-transformed, whilst *y*-axes for total storages of nitrogen and carbon are log-transformed. C, control; Fl, foliar insecticide; Sl, soil insecticide; Fl+Sl, both compounds. Values reported at the top of each graph are *P* values from ANOVA for the effects of insecticide applications and their interactions.

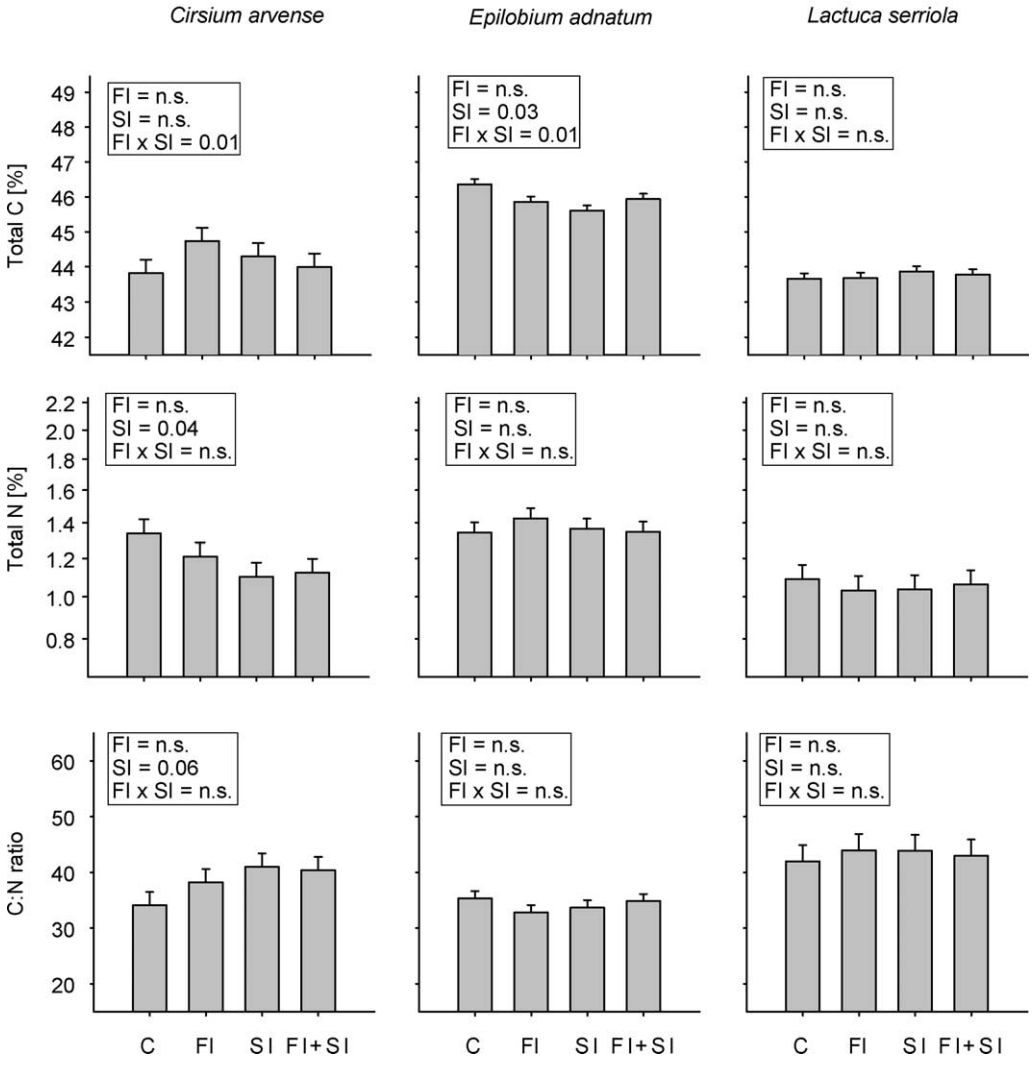

Fig. 2. Effects of insecticide application on concentration of carbon and nitrogen of three common plant species on the experimental plots (means ± standard error). Note that *y*-axes for total nitrogen and carbon are arcsin-transformed. C, control; FI, foliar insecticide; SI, soil insecticide; FI + SI, both compounds. Values reported at the top of each graph are *P* values from ANOVA for the effects of insecticide applications and their interactions.

N content in roots, but not in the combination treatment (significant interaction between insecticide treatments). As a result of increased root biomass, the total C and N storage in roots increased with the application of soil insecticide (Fig. 1).

With the application of soil insecticide, we found a lower C content in the litter of *E. adnatum* (Fig. 2). However, this effect was rather weak (−1.5%) and disappeared in treatments where we applied the two insecticides simultaneously (significant interaction between soil and foliar insecticide). In contrast, N content of the litter of *C. arvense* decreased with the application of soil insecticide (−12%) and consequently we found a higher C:N ratio. Litter quality of *L. serriola* was not affected by application of insecticides.

3.2. Decomposition

Initial leaf dry mass as well as total cover abundance of vegetation affected the decomposition rate of leaf material in litter bags negatively (ANCOVA, dry mass: $F_{1,25}=5.08$, $P=0.03$; cover abundance: $F_{1,25}=7.50$, $P=0.01$). Both parameters were therefore included in the analysis as covariates. Decomposition rates increased with the application of foliar insecticide (corrected means ± standard error, without: 56.7 ± 0.01%, with: 60.5 ± 0.01%, ANCOVA, $F_{1,25}=8.51$, $P=0.007$). However, this difference accounts for 4% of initial dry mass only. Application of soil insecticide did not affect decomposition rates (without: 58.0 ± 0.01%, with: 59.1 ± 0.01%, ANCOVA, $F_{1,25}=0.86$, $P>0.3$).

3.3. Soil parameters

In August 1998, the application of soil insecticide caused a slight, but significant increase of soil water content from 13.9 to 14.3% (ANOVA, $F_{1,81}=6.03$, $P=0.02$). Soil water content was negatively correlated to total cover abundance

of vegetation in the plots in August ($r = -0.66, P < 0.001$). In the control plots and the treatment with foliar insecticide, the dominant *E. adnatum* reached its maximum in cover abundance during August, whereas *C. arvense*, which dominated the plots with soil insecticide, reached its maximum in cover abundance during early July. This resulted in a higher total cover abundance in August on the former plots. Therefore, differences of soil water content between treatments may be due to a different phenology of communities on the plots contingent on the dominant species.

In general, C and N content of soil increased during the first two years of succession, indicating an accumulation of organic matter in the soil. Both parameters were closely correlated across all plots ($r = 0.65$; $P < 0.001$). Across all sampling dates, there was no overall effect of the insecticide application on the contents of N and C, and on C:N ratio in the soil (ANCOVA, all $P > 0.1$). However, the application of soil insecticide decreased the accumulation of C until June of the second year (significant soil insecticide × time interaction, ANCOVA, $F_{1,91} = 5.0$, $P = 0.03$). This effect did not persist and disappeared at the end of the growing season.

The application of soil insecticide caused a 30% increase in the content of nitrate (Fig. 3, ANCOVA, $F_{1,80} = 30.18$, $P < 0.001$) and total available nitrogen in soil both in late spring and late summer of the second year (Fig. 3, ANCOVA, $F_{1,80} = 30.84$, $P < 0.001$). This effect was stronger in late summer, as indicated by the significant interaction

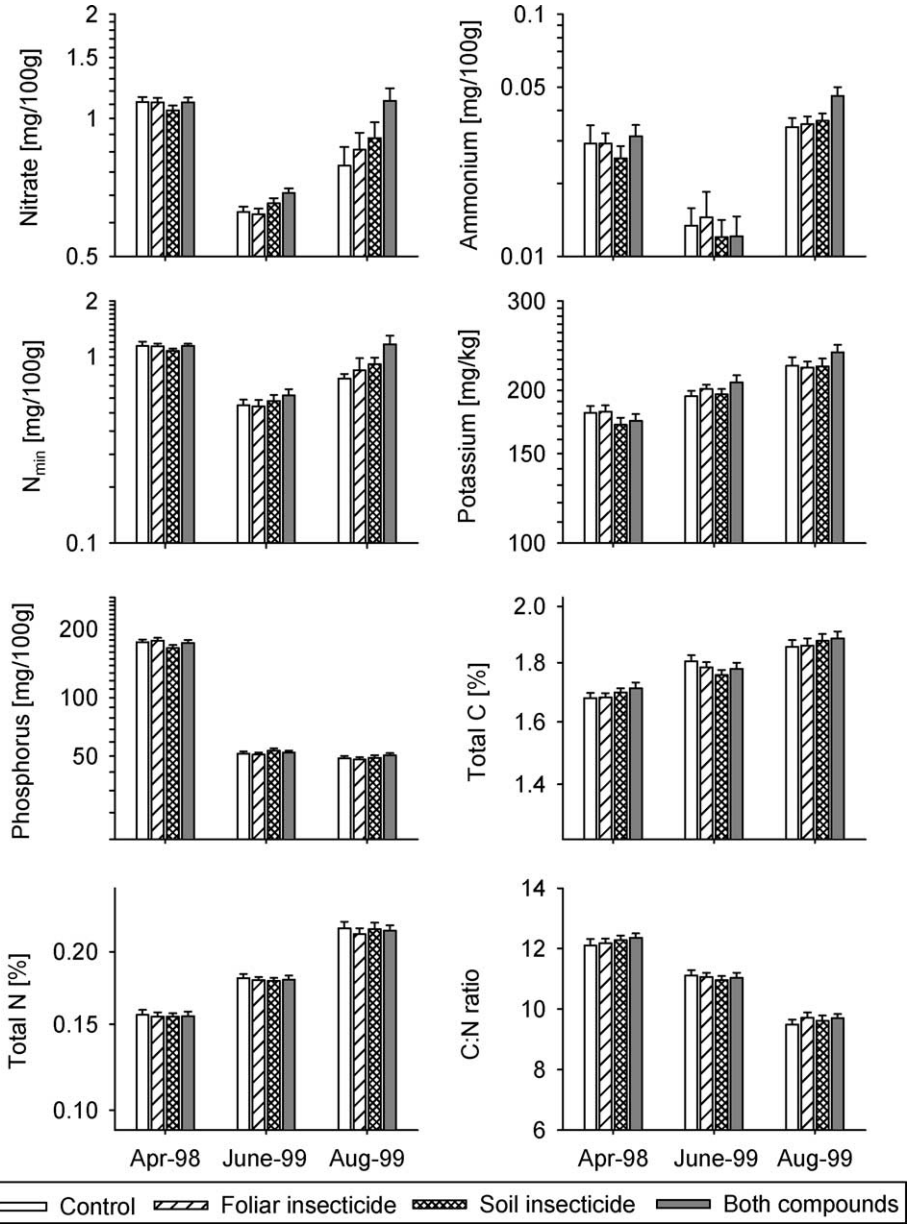

Fig. 3. Effects of insecticide application on the concentration of soil nutrients, carbon and nitrogen. Note that *y*-axes for total nitrogen and carbon are arcsin-transformed, whilst *y*-axes for nutrient concentrations are log-transformed.

soil insecticide×time (ANCOVA, $F_{1,91}=6.81$, $P=0.01$, respectively, $F_{1,91}=6.93$, $P=0.01$). Applying both insecticides to the experimental plots resulted in a further increase of available N content (significant soil insecticide×foliar insecticide interaction, ANCOVA, $F_{1,91}=7.47$, $P=0.01$). Furthermore, the application of soil insecticide increased the content of potassium in the soil (Fig. 3, ANCOVA, $F_{1,80}=3.82$, $P=0.05$). However, this effect was rather small (+4%). The content of available phosphor was not affected by insecticide application.

Contents of available nitrogen depended from the development of vegetation. N_{min}, ammonium and nitrate in the soil decreased with increasing plant biomass during the growing season, whereas the decline of vegetation caused an increase of available nitrogen in late summer (Fig. 3). The change of total cover abundance in the period from June to August was negatively correlated with the change of available nitrogen ($r=-0.27$, $P=0.02$). Thus, the temporary lower cover abundance on plots with treated with soil insecticide is associated with a temporary increase of N_{min} (Fig. 3). This lower cover abundance is due to the lack of *E. adnatum* on these plots, which showed a late biomass peak in August and dominated the plots without soil insecticide. Accordingly, cover abundance of *E. adnatum* was negatively correlated to N_{min} ($r=-0.43$, $P=0.006$).

3.4. Microflora

Basal respiration and microbial biomass differed little between the two sampling dates. Microbial biomass and activity were higher in the upper soil horizon. Neither basal respiration nor microbial biomass or qCO_2 of any soil horizon was affected by the application of insecticides at the two dates (all $P>0.05$). However, at the first sampling date in April, basal respiration in the upper horizon was positively correlated to above-ground biomass ($r=0.47$, $n=20$, $P=0.03$) and mean cover abundance ($r=0.34$, $n=40$, $P=0.03$) on the plots in the previous year. This was also evident for the microbial biomass with a positive correlation to above-ground biomass ($r=0.38$, $n=20$, $P=0.09$) and mean cover abundance ($r=0.42$, $n=40$, $P=0.007$). In May, basal respiration and microbial biomass were still significantly correlated to mean cover abundance in the previous year ($r=0.32$, $P=0.04$, respectively, $r=0.31$, $P=0.05$). For the lower horizon microbial parameters were not correlated to cover abundance. Further, root biomass in the previous year did not affect soil microflora.

4. Discussion

4.1. Above-ground vegetation and storage of C and N in litter and roots

Even if differences between means of plant biomass of the treatments were high, means were associated with high standard errors. However, a negligible effect of insecticide application on above-ground plant biomass on a highly productive would support ideas on the relationship between the strength of herbivore effects and site productivity (Oksanen et al., 1981; Fraser and Grime, 1997), although if the applicability of this idea to invertebrates is still debatable (Oksanen and Oksanen, 2000; Wardle, 2002; Schädler et al., 2003a).

By changing quality and quantity of plant tissue, herbivores may affect the cycling of nutrients (Bardgett et al., 1998; McNaughton et al., 1989). Tissue loss often results in compensatory responses of plants and an increased mobilization of nutrients (see Bardgett et al., 1998, for review). The application of foliar insecticide, however, did not increase N content in the litter of the three species investigated in our study. Similarly, root herbivory may induce physiological changes in plant tissue leading to an increase in N and carbohydrates (Gange and Brown, 1989; Masters et al., 1993). According to Masters et al. (2001), this relative increase of nutrients is a response to a water stress induced by damage of roots by herbivores. *C. arvense* increased in abundance on plots with soil insecticide (Schädler et al., 2004). Furthermore, *C. arvense* decreased its N content in senescent leaves with the application of soil insecticides, which supports the above idea.

Root herbivory may result in a loss of C due to increased respiration or simple leakage of carbohydrates from damaged roots (Brown and Gange, 1990). Accordingly, C content of roots and total below-ground C storage increased with the application of soil insecticide in our study. In contrast, the increase of total below-ground N was simply due to higher root biomass. The application of foliar insecticide had no effect on root C or N.

4.2. Decomposition

Usually, it is assumed that the activity of arthropods speeds up decomposition. Beside the direct consumption of dead plant material by primary decomposers, indirect effects of secondary decomposers on decomposing microflora often play an important role in the cycling of nutrients in natural systems. In our study, exclusion of above-ground insects increased the decomposition of leaves of *C. arvense* on the experimental plots. Insecticides may function as an additional C-source, which may increase the C:N ratio of leaves. However, this should decrease decomposition rate. Therefore, and due to the minute amount of C introduced with insecticide, we assume that the insecticides per se had little influence on our results. The most likely explanation for the higher decomposition rate with the application of foliar insecticide may be the impact of insecticide on epigeic invertebrate predators. This may have a positive effect on densities of destruents (Kajak, 1997; Lawrence and Wise, 2000), which are less exposed to above-ground application of insecticides. Similarly, Edwards et al. (1967),

Edwards and Thompson (1973) and Pimentel and Edwards (1982) showed that insecticide application sometimes may have stronger effects on predatory arthropods and therefore increase numbers of springtails and mites with indirect effects on decomposition of organic matter. However, abundance and community composition of mites was not affected significantly by insecticide application at our field site (Endlweber and Scheu, unpublished). In general, the effect of insecticide application on decomposition rate was rather small in our study and should have little ecological importance in nutrient rich habitats.

4.3. Soil parameters

During the second growing season the application of soil insecticide caused a higher availability of soil water and N_{min}. These changes were triggered by changes of the seasonal dynamics of the different communities, which developed on the experimental plots. In August, soil water was negatively correlated with total cover abundance. This may be explained with the water requirements of an increased biomass and losses due to interception as well as evapotranspiration. Plots treated with soil insecticide and dominated by the creeping thistle, which died back already in early August had a lower cover abundance at the second sampling date than plots dominated by the Willow herb, which persisted about a month longer. These phenological differences coincide with the differences in the availability of N_{min} in soil. Thus, mineralization of nitrogen was highest on those plots where the decline of living phytomass during the season was highest. This indicates that the mineralization depends on litter input and nutrient uptake by the vegetation. Other traits of the involved species may have amplified this effect. For example, *C. arvense* sheds its litter immediately after senescence of leaves and produces large quantities of pappi (see also Zagt, 1997) whereas the litter of *E. adnatum* adheres to the stem until winter. Additionally, the higher below-ground C and N storage with the application of soil insecticide may have increased nitrogen mineralization (Coleman et al., 1983). We conclude that an increased content of available nitrogen in soil may be due to changed vegetation dynamics caused by root herbivory. In contrast to our results, mineralization of nutrients can sometimes be reduced by insecticide application mainly due to negative effects on the decomposer fauna (Pimentel and Edwards, 1982).

We are aware that applying chemical compounds like insecticides may directly increase the nutrient content in the soil. However, chlorpyrifos is an organophosphate and does not contain any nitrogen but may increase soil phosphorus. Following Domsch (1992), chlorpyrifos is not degrading to plant available phosphorus. Further, McGonigle and Fitter (1988) showed that the application of the chemically related compound Chlorfenvinphos did not affect the content of phosphorus in *Holcus lanatus*. Accordingly, we did not detect any changes in soil phosphorus with the application of soil insecticide.

Microbial biomass and activity show a strong relationship to structural and functional traits of plant communities (Wardle and Nicholson, 1996; Wardle and Barker, 1997; Bardgett and Shine, 1999; Bardgett et al., 1998; Wardle et al., 1999, 2000). Effects of herbivores on resource dynamics may therefore be reflected in the soil microflora. However, the application of both insecticides did not affect microbial biomass or activity in soil at the beginning of the third year. This was also true immediately after the insecticide applications in spring. Across all treatments, however, these parameters were positively affected by plant biomass and total cover abundance in the previous year. Wardle (2002), Zak et al. (1994) and Wardle and Barker (1997) point at an overriding importance of plant biomass production for the soil microflora. In our study, this effect was restricted to the upper horizon (0–3 cm). We conclude that invertebrate herbivory may affect soil microflora through changes of standing plant biomass.

5. Conclusion

The availability of nutrients and other resources are crucial determinants for growth and fitness of plants as well as for interactions between plant species. Insect herbivory induced changes of structure and dynamics of plant communities (Brown and Gange, 1989; Fraser and Grime, 1997; Wilcox, 1998; Schädler et al., 2004) may induce changes in resource dynamics. Hence, the outcome of an exclusion experiment may be in part the result of changed resource availability and not only the result of direct effects of herbivores on plants. A further issue arises from the use of insecticides, which usually kill all insects. The importance of non-phytophagous soil insects as an interface between above- and below-ground processes and as a trigger of nutrient turnover in ecosystems is beyond doubt (Wardle, 2002). Killing these insects with soil insecticides may result in a reduced nutrient availability, again with effects on the vegetation. Nevertheless, our study suggests, that rather than changes of the quality in organic matter input, changes of the community composition due to root herbivory influence the nutrient dynamics. Thereby, the phenology and other traits of involved plant species are the key to understand the resource dynamics in the soil.

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