ABOVE- AND BELOWGROUND INTERACTIONS ARE MEDIATED BY NUTRIENT AVAILABILITY

Josephine Haase,[1,3] Roland Brandl,[1] Stefan Scheu,[2] and Martin Schädler[1,4]

[1]*University of Marburg, Faculty of Biology, Department of Animal Ecology, Karl-von-Frisch-Strasse 8, 35032 Marburg, Germany*
[2]*University of Darmstadt, Department of Biology, Animal Ecology, Schnittspahnstrasse 3, 64287 Darmstadt, Germany*

Abstract. By influencing nutrient mineralization in the soil, decomposers may affect the performance of plants and their associated herbivores. The strength of above–belowground linkages may therefore depend on the availability of nutrients in ecosystems. We investigated the dependency of decomposer- and leaf-herbivore-mediated changes in plant performance on soil nutrient availability in microcosm systems. In separate treatments, *Poa annua* was used as host plant for the herbivore and was grown in combination with different herb species: *Plantago lanceolata*, *Trifolium repens*, and *Sanguisorba minor*. At three different levels of nutrient availability, the impact of Collembola (*Folsomia candida*) and aphids (*Rhopalosiphum padi*), as well as their interacting effects on plant performance, were investigated. We further assessed the effects of Collembola on the performance of aphids and vice versa, as well as the effects on element contents in *P. annua* and soil nutrients.

Collembola increased total aboveground biomass and biomass of single plant species (except *T. repens*) only at low and moderate nutrient availability, whereas the negative effects of aphids on *P. annua* and total aboveground biomass were highest at high nutrient availability. Collembola decreased relative root allocation. The negative effect of aphids on plant biomass was more pronounced in the presence of Collembola. Nitrogen concentration in shoots of *P. annua* was increased by Collembola. Aphids decreased the nitrogen concentration in grass shoots only when Collembola were present. These interacting effects can be related to indirect effects of decomposers on herbivore performance. At low and moderate nutrient availability, aphid numbers strongly increased due to decomposers, whereas at high nutrient availability this effect was much weaker. In turn, aphid herbivory increased the number of Collembola only at high nutrient availability.

We conclude that the role of both below- and aboveground food webs for the dynamics of vegetation depend on each other and the availability of nutrients in ecosystems. This suggests that nutrient enrichment of ecosystems may have important consequences for above–belowground linkages and their effects on natural communities.

Key words: above-belowground linkages; decomposers; herbivores; microcosms; nutrient availability; plant communities; trophic interactions.

INTRODUCTION

Biotic interactions in the soil, particularly in the plant's rhizosphere, affect not only the growth and competitive ability of plants but also consumers associated with them (Wardle et al. 2004). By mobilizing nutrients and stimulating their uptake by the plant, the soil fauna affects aboveground herbivores (Scheu et al. 1999, Bonkowski et al. 2001, Wurst and Jones 2003, Newington et al. 2004). Arthropods, and in particular Collembola, are of great importance in the decomposer food web (Petersen and Luxton 1982, Petersen 2002). Collembola are present in almost all terrestrial ecosys-

tems (Hale 1967, Peterson and Luxton 1982), and are the dominating group of fungivores (Hopkin 1997, Peterson 2002). Since fungal mycelia are rich in nitrogen, grazing by Collembola is important for the nitrogen budget (Lussenhop 1992, Scheu et al. 1999, Bakonyi et al. 2002). Furthermore, Collembola may affect plants indirectly through processes such as mineralization and redistribution of nutrients and by modifying the root environment as well as soil structure (Filser 2002, Scheu and Setälä 2002). Last but not least, Collembola play an important role as shredders of litter and in humus formation (Rusek 1985). However, the effects of Collembola on nutrient cycling and plant growth can be positive (Gange 2000, Kreuzer et al. 2004, Lussenhop and BassiriRad 2005), neutral (Larsen and Jakobsen 1996, Gormsen et al. 2004), or negative (Schütz et al. 2008). Some studies showed that Collembola affect aboveground leaf herbivores, such as aphids (Scheu et al. 1999, Schütz et al. 2008). Collembola may indirectly affect performance of leaf herbivores through physio-

logical processes within their host plants, such as changes in the nutritional status and chemistry and hence plant defense mechanisms (Scheu et al. 1999).

Leaf herbivores affect the competitive ability of plants and thereby the structure of plant communities (Crawley 1997, Fraser and Grime 1997, Carson and Root 1999), which may feed back on the decomposer community (Salamon et al. 2004, Milcu et al. 2006). The effects of herbivory may vary with the availability of soil nutrients (Fraser and Grime 1999), since nutrients affect rates of herbivory and the ability of plants to respond to herbivory (Throop 2005). Up to now, the few studies investigating the interacting effects of herbivory and nutrient availability on plant growth ignored changed consumption rate and population growth of herbivores as affected by the nutritional status of plants (see Throop 2005). Previously, we showed that such changes in host quality (induced by interspecific plant competition) triggered the impact of herbivores on their hosts (Schädler et al. 2007b). Furthermore, leaf herbivores may influence processes in the soil through changes in plant biomass, quality and resource allocation (Bardgett and Wardle 2003, Wardle et al. 2004). Overall, these linkages between decomposers and leaf herbivores are highly dynamic and influence the structure of plant communities even on shorter time scales (Bardgett et al. 2005). We are not aware of any study demonstrating consequences of interactions between decomposers and aboveground herbivores for plant performance and community structure.

Previous studies on the ecosystem role of decomposers ignored the effects of nutrient availability and used soils where nutrients were leached to accentuate the effects of decomposers (e.g., Scheu et al. 1999, Kreuzer et al. 2004, Partsch et al. 2006). Little is known about the relative importance of decomposers at sites with a higher nutrient availability. Parallel to their effect on plant performance, indirect effects of decomposers on plant associated herbivores are likely to vary with nutrient availability, with possible feedbacks on the top-down control of plant communities. Since nitrogen is one of the main limiting factors for leaf herbivores (Mattson 1980, Dixon 1998, Schädler et al. 2007a), we hypothesize that the activity of decomposers and nutrient addition will enhance their performance. Both factors should interact, with the relative importance of nutrient supply for herbivore performance and plant growth due to decomposer activity being less pronounced at a higher soil nutrient availability. Furthermore, since decomposers and aphids may affect each other, we hypothesize that their effects on the plant community also interact. We designed an experiment to investigate the interactions between nutrient availability, decomposers and leaf herbivores on experimental plant assemblages. The aim of our study was to test the following hypotheses: (1) positive effects of decomposers on plant growth and herbivore performance are more important at levels of low nutrient availability; (2) performance of herbivores and therefore their effects on plant growth and decomposers is highest at high nutrient availability; (3) the effects of decomposers on herbivore performance result in a changed top-down effect of decomposers on the vegetation.

METHODS

Experimental design

We established a microcosm experiment with plant assemblages consisting of species typical for central European grasslands and which differ in nutrient requirements. The annual grass *Poa annua* (L.) was used as the host species for the herbivore and was present in all microcosms. We established different treatments with one of the following three plant species as potential competitors with *Poa annua*. The herb *Plantago lanceolata* (L.) occurs across a wide gradient of nutrient availability, *Sanguisorba minor* (Scop.) is a typical meadow herb on poor to moderately fertile soils and *Trifolium repens* (L.) is a nitrogen-fixing legume. The bird cherry-oat aphid *Rhopalosiphum padi* (L.) (Homoptera: Aphididae) was used as an herbivore. This aphid species is heteroecious and holocyclic with sexual stages. It shows host plant alternation with *Prunus padus* (L.) as primary and various grasses as secondary hosts (Dixon 1971). *Poa annua* is its only host plant in the species pool of plants in our experiment. As a decomposer species we used *Folsomia candida* (Willem) (Collembola, Isotomidae) which is known to feed on saprophytic fungi (Klironomos et al. 1999).

In January 2005, seeds of the four plant species were sown into pots in the greenhouse. Day length was maintained at 12 h with supplementary light (sodium lamps, 400 W; Philips Son-T Agro, Eindhoven, The Netherlands). Temperature varied between 15°C (night) and at maximum 28°C (day). After three weeks, three seedlings of each of the two plant species in the different combinations were transplanted into microcosms consisting of PVC tubes (inner diameter 10.4 cm, height 20 cm), closed at the bottom with gauze (100-μm mesh). Soil was taken from an old fallow grassland site (Lahnberge near Marburg; Hesse, Germany; 50°48′ N, 8°48′ E, 325 m above sea level) and, prior to use, was defaunated by freezing at −20°C for seven days (Huhta et al. 1989). After a further seven days, three subsets of 30 L soil were irrigated by adding three times 10 L of deionized water to each every two days to leach the nutrients which were released as a result of the defaunation process. The soil was mixed with sand (v/v ratio 1:1), resulting in initial nutrient contents of 6.3 mg NO_3^- and 0.45 mg NH_4^+ per kg soil (dry mass) (determined from pooled subsamples). These values correspond to the nutrient availability of nutrient-poor agroecosystems.

Microcosms were filled to a height of 6 cm with sand (for drainage) and with 1 L of the soil mixture. An experimental gradient of nutrient availability was established by adding a slow-release NPK fertilizer

(Basacote Plus 3M, 16-8-12 NPK, coated with trace elements; Compo, Münster, Germany) to the soil. At the low level of nutrient availability, no fertilizer was applied, while at the moderate and high levels of nutrient availability 0.2 g and 2.0 g of fertilizer per liter of soil were added, respectively. These nutrient additions correspond to agricultural application rates of 38 kg N/ha (weak fertilization rate) and 380 kg N/ha (strong fertilization rate). Five grams (±0.2 g; mean ± SE) of litter (grassland swath, consisting mainly of grass leaves) were placed on top of the soil as the food source for the Collembola. The swath (carbon content 42.06%, nitrogen content 1.12%) was collected in October 2004, dried at 30°C and cut into pieces of about 2 cm in length.

Two weeks after transplanting the seedlings, 40 individuals of F. candida from laboratory cultures were added to half of the microcosms. Each microcosm was equipped with a ring of transparent vitrification foil of 20 cm height to prevent the escape of the Collembola. After a further six weeks, five nymphs of R. padi were added to half of the microcosms. To prevent the escape of aphids, the top of all microcosms were closed with polythene bags (height 20 cm). Two windows (15 × 10 cm) were cut into the bags and closed with gauze (200-μm mesh) to allow for ventilation.

The experiment was set up in a full-factorial design, with three levels of nutrient availability, three levels of plant composition, decomposers (with/without Collembola), and leaf herbivores (with/without aphids). All 36 possible treatment combinations were replicated five times. Microcosms were randomly assigned to five blocks and randomized within the blocks every week. All microcosms were irrigated every two days with 100 mL of water.

After a further three weeks, the plants were harvested. In decomposer-microcosms, one soil core (diameter 5.7 cm, depth 10 cm) was taken. Collembola were extracted by heat from the soil. Roots from the soil cores and the remaining soil material of all microcosms were washed. Stone- and root-free soil samples were sealed in polythene bags and stored at −25°C for subsequent analyses. Above- and belowground plant material was dried at 60°C to constant mass and subsequently weighed to the nearest 0.1 mg. Root biomass could not be determined according to species and was pooled. Additionally, shoots of P. annua were ground in a mill and three subsamples per microcosm were analyzed for carbon and nitrogen content using an Elementar Vario EL element analyzer (Elementar Analysengeräte GmbH, Hanau, Germany). For further analyses, these data were averaged across subsamples.

The aphids were removed from the plants and stored in alcohol. In samples with large numbers of aphids, we estimated their numbers from subsamples by spreading the aphids on a petri dish and counting them within at least 10 1-cm² squares (at minimum we counted 20 individuals). The total number of aphids was then estimated by extrapolating the counts to the total area of the petri dish. Winged and wingless aphids were counted separately.

Concentrations of nitrate and ammonium in the soil were determined photometrically after extraction with calcium chloride solution (Spectroquant NOVA 400; Merck, Darmstadt, Germany). Fifty grams per soil sample were mixed with 100 mL of 0.025 mol/L calcium chloride solution on a shaker for 1 h. The solution was filtered through a fluted filter. NH_4^+-N in the extracts was determined spectrophotometrically after formation of indophenol blue by reaction in alkaline solution with a chlorinating agent and thymol (Spectroquant Ammonium-test, Merck). NO_3^--N was determined by formation of 4-nitro-2,6 dimethylphenol with sulphuric acid and 2,6-dimethylphenol (Spectroquant Nitrate-test, Merck).

Statistical analyses

If necessary, biomass data were log-transformed prior to analyses to achieve a normal distribution of residuals. Data on the total number of Collembola were also log-transformed, whereas normal distribution of residuals was best achieved by a square-root transformation in the case of the number of aphids. The proportion of winged aphids was arcsine-square-root transformed. Data on soil nutrients were log-transformed. If data were log-transformed, means in the text are given as back-transformed values and the variance around the mean as lower limit (ll) = back-transformed (mean − standard error) and upper limit (ul) = back-transformed (mean + SE).

The effects of block, nutrient availability, decomposers, aphids, and plant composition on the total plant biomass and biomass of P. annua, ammonium, and nitrate in the soil and carbon and nitrogen concentrations in grass shoots were analyzed by a five-way ANOVA (GLM procedure in SPSS 12.0). Relative root allocation was analyzed with root biomass (log) as the response variable and shoot biomass (log-transformed) as a covariate (Müller et al. 2000). The effects of block, nutrient availability, decomposers, and aphids on the growth of the competitors (Pl. lanceolata, S. minor, T. repens) as well as the effects of block, nutrient availability, decomposers, and plant composition on the development of aphids were tested using a four-way ANOVA. The effects of grass biomass and nitrogen concentration in shoots on the number of aphids, as well as the effects of nitrogen concentration on the proportion of winged aphids, were analyzed by inclusion as covariates in an ANCOVA. By using type I sums of squares, the effects of the treatments were tested after removing possible effects of biomass and the nutritive status of the host plant. Similarly, the effects of plant biomass and soil water content on population size of Collembola were analyzed by ANCOVA. The effects of block, nutrient availability, aphids and plant composition on the development of Collembola were analyzed using a four-way ANOVA. In all analyses, interactions
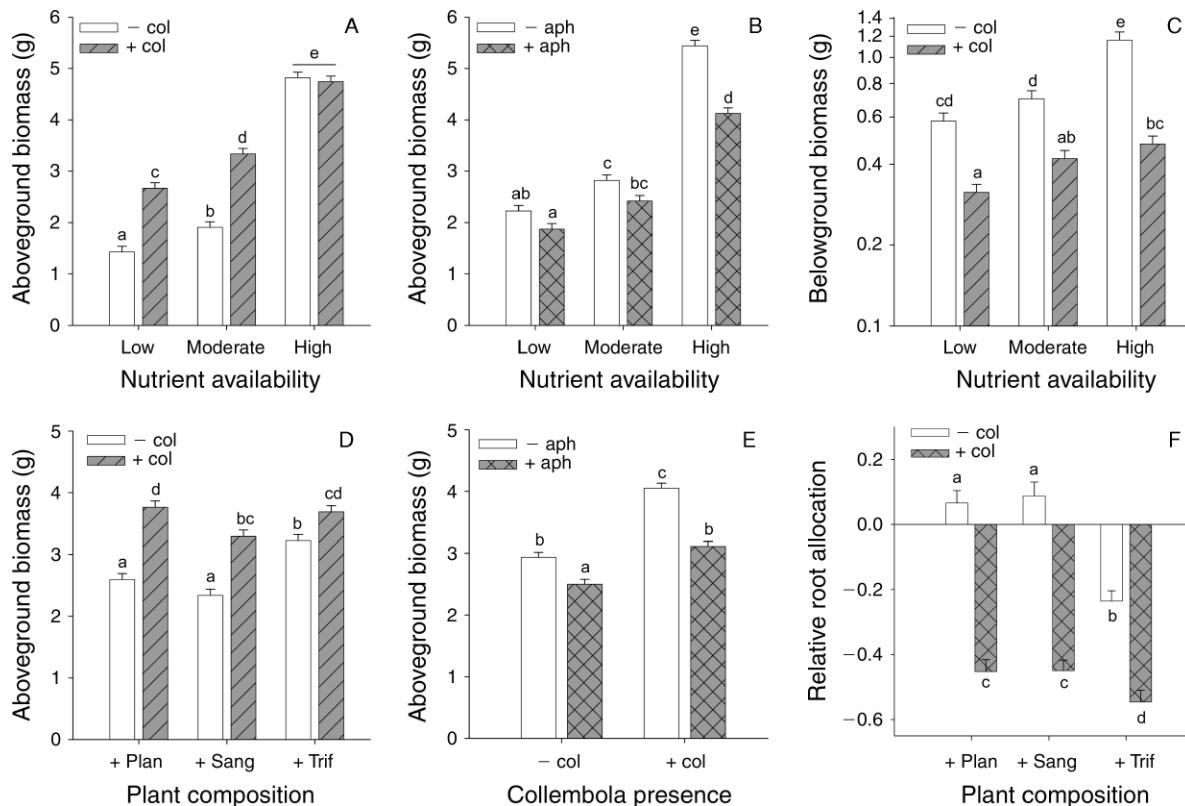
FIG. 1. Effects on the (A, B, D, E) aboveground biomass, (C) belowground biomass, and (F) relative root allocation of the plant assemblages in the microcosms. Relative root allocation is given as log(root biomass) per unit log(shoot biomass). Abbreviations are: col, Collembola; aph, aphids. Plant composition: *Poa annua* with *Plantago lanceolata* (+ Plan), *Sanguisorba minor* (+ Sang), or *Trifolium repens* (+ Trif). Values are means + SE. The *y*-axis for belowground biomass (C) is a log scale. Significant differences between means are denoted with different letters above the bars following Tukey's hsd post hoc test ($P <$ 0.05). For statistical analyses, see Table 1.

with the factor block were pooled into the error term (Newman et al. 1997). Every ANOVA with significant interaction terms was followed by a post hoc test (Tukey's hsd).

Results

Total plant biomass

Nutrient addition increased total plant shoot and root biomass (Fig. 1A–C, Table 1). The increase in shoot biomass in the presence of Collembola diminished with increasing levels of nutrient availability (Fig. 1A, Table 1). In contrast, aboveground biomass was negatively affected when grown with aphids only at the level of highest nutrient availability (Fig. 1B, Table 1). Belowground biomass was unaffected by the presence of aphids, but decreased with the activity of Collembola especially at the highest nutrient availability (Fig. 1C, Table 1). The increase of aboveground biomass in the presence of Collembola differed between the plant composition treatments (Fig. 1D, Table 1). Assemblages consisting of *P. annua* and *Pl. lanceolata* benefited most, whereas assemblages of *P. annua* and *T. repens* were least affected by the presence of Collembola. The

decrease of aboveground biomass observed with aphids, however, was strengthened in the presence of Collembola (Fig. 1E, Table 1) and was not dependent on plant species composition or nutrient availability. Relative root allocation was lower in the presence of Collembola, depending on plant species composition (Fig. 1F, Table 1). When Collembola were absent, relative root allocation was lowest in assemblages with *T. repens*, an effect which was much weaker in microcosms with Collembola. The Collembola-mediated decrease in relative root allocation was strongest when *P. annua* grew together with *Pl. lanceolata* or *S. minor*.

Individual plant species

Shoot biomass of *P. annua* increased with increasing nutrient availability (Fig. 2A, Table 1). Collembola increased biomass of grass shoots only at moderate nutrient availability (Fig. 2A, Table 1). Furthermore, the presence of aphids decreased shoot biomass of their host plant *P. annua*, which was, however, only significant at high nutrient availability (Fig. 2B, Table 1). Effects of Collembola and aphids interacted with each other; Collembola increased grass shoot biomass

TABLE 1. Results of the ANOVA (*F* values) of the effects of plant species composition (PS), nutrient availability (NU), Collembola (CO), and aphids (A) on plant community growth and on aboveground biomass and aboveground concentration of carbon and nitrogen of *Poa annua*.

		Community			*Poa annua* aboveground		
Source of variation	df	Shoot biomass	Root biomass	Root allocation	Shoot biomass	Carbon (%)	Nitrogen (%)
Plant composition (PS)	2, 140	17.54***	8.01**	20.66***	4.95**	1.40	1.28
Nutrient availability (NU)	2, 140	356.12***	25.19***	2.07	151.11***	15.57***	11.93***
Collembola (CO)	1, 140	95.86***	110.20***	131.48***	9.18**	0.11	363.84***
Aphids (A)	1, 140	60.92***	2.56	1.00	23.56***	4.61*	24.12***
CO × A	1, 140	8.23**	0.78	3.16	7.28**	1.53	11.09**
PS × CO	2, 140	5.57**	0.83	6.54**	0.47	0.10	2.29
PS × A	2, 140	0.12	1.12	1.48	0.10	0.40	0.73
NU × CO	2, 140	28.77***	3.15*	2.04	6.15**	20.67***	6.92**
NU × A	2, 140	12.63***	1.38	1.15	6.56**	0.62	1.23
PS × NU	4, 140	4.77**	1.60	1.08	1.16	0.17	2.01
PS × CO × A	2, 140	0.99	1.74	2.42	1.08	2.55	0.89
NU × CO × A	2, 140	0.82	1.03	1.55	0.74	0.27	0.88
PS × NU × CO	4, 140	1.18	0.87	1.85	2.52*	0.90	1.45
PS × NU × A	4, 140	0.72	1.96	0.64	3.00*	1.95	0.36
PS × NU × CO × A	4, 140	0.74	0.20	0.20	0.51	0.81	0.91

 * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001.

only in the absence of aphids (Fig. 2C, Table 1). Nitrogen concentration in shoots of *P. annua* increased in the presence of Collembola at all levels of nutrient availability, with the strongest effects at low and

moderate levels (Fig. 2D, Table 1). Nitrogen concentration was equally high at all levels of nutrient availability in microcosms with Collembola. Aphids decreased nitrogen concentration in grass shoots only in the
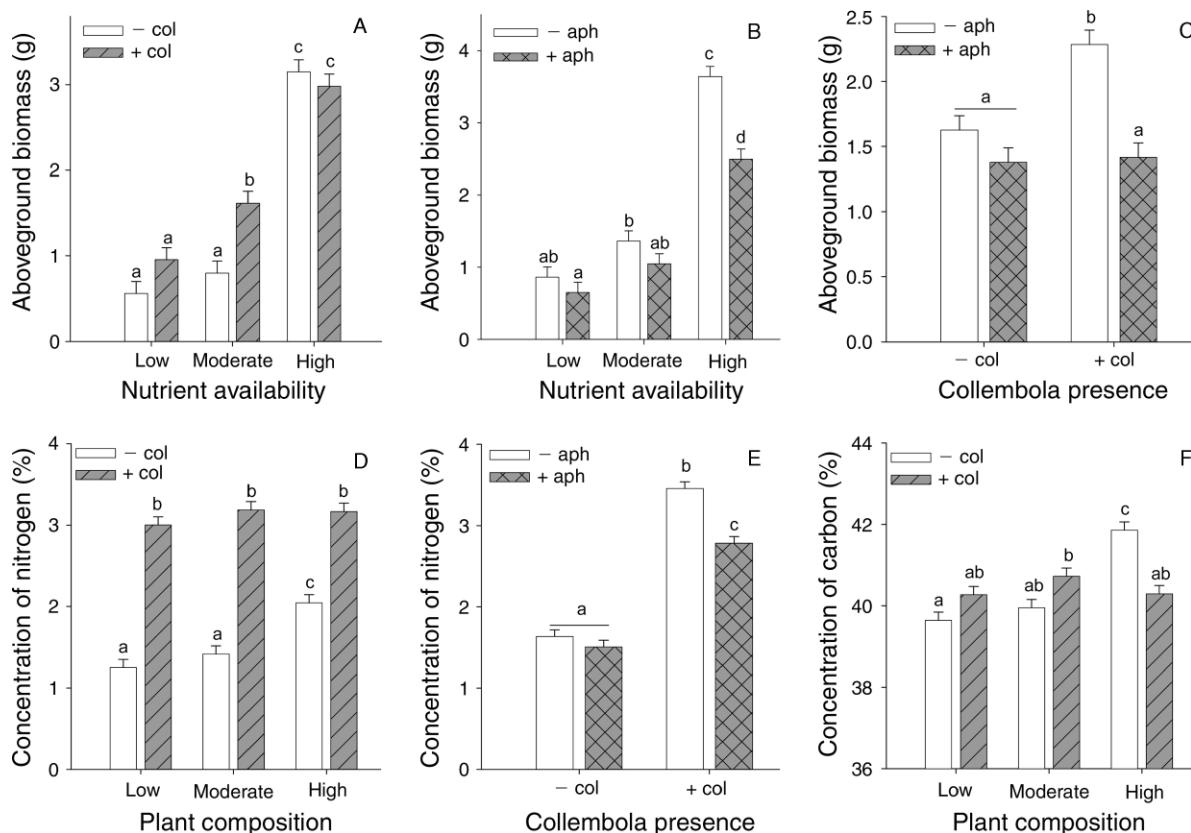

FIG. 2. Effects on the (A, B, C) aboveground biomass and (D, E, F) element concentrations in the shoots of *Poa annua*. Abbreviations are: col, Collembola; aph, aphids. Values are means + SE. Significant differences between means are denoted with different letters above the bars following Tukey's hsd post hoc test (*P* < 0.05). For statistical analyses, see Table 1.

TABLE 2. Results of the ANOVA (*F* values) of the effects of nutrient availability (NU), Collembola (CO), and aphids (A) on aboveground growth of *Plantago lanceolata*, *Sanguisorba minor*, and *Trifolium repens*.

Species	Nutrient availability (NU) (df = 2, 44)	Collembola (CO) (df = 1, 44)	Aphids (A) (df = 1, 44)	CO × A (df = 1, 44)	NU × CO (df = 1, 44)	NU × A (df = 1, 44)	NU × CO × A (df = 1, 44)
P. lanceolata	10.65***	36.19***	0.08	0.06	9.23***	1.05	0.05
S. minor	22.04***	23.29***	0.35	1.86	18.24***	0.19	4.77*
T. repens	0.78	0.93	0.72	0.43	2.88	2.33	1.21

 * *P* < 0.05; *** *P* < 0.001.

presence of Collembola (Fig. 2E, Table 1). Collembola decreased carbon concentration in shoots of *P. annua* at high nutrient availability only (Fig. 2F, Table 1).

In microcosms without Collembola, shoot biomass of *Pl. lanceolata* and *S. minor* increased with nutrient addition (all means back-transformed values; for low nutrient availability, *Pl. lanceolata* mean = 0.43 g, ll [lower limit of back-transformed standard error, see *Statistical analysis*] 0.32 g and ul [upper limit] 0.57 g; *S. minor* mean = 0.36 g, ll 0.27 g and ul 0.48 g; for moderate nutrient availability, *Pl. lanceolata* mean = 0.84 g, ll 0.63 g and ul 1.12 g; *S. minor* mean = 0.75 g, ll 0.56 g and ul 0.99 g; for high nutrient availability, *Pl. lanceolata* mean = 1.48 g, ll 1.11 g and ul 1.97 g; *S. minor* mean = 2.04 g, ll 1.53 g and ul 2.70 g). Both plant species benefited from Collembola activity only at low and moderate levels of nutrient availability (Collembola microcosms: for low nutrient availability, *Pl. lanceolata* mean = 1.49 g, ll 1.12 g and ul 1.98 g; *S. minor* mean = 1.20 g, ll 0.91 g and ul 1.60 g; for moderate nutrient availability, *Pl. lanceolata* mean = 1.90 g, ll 1.43 g and ul 2.53 g; *S. minor* mean = 1.77 g, ll 1.34 g and ul 2.35 g; for high nutrient availability, *Pl. lanceolata* mean = 1.53 g, ll 1.15 g and ul 2.05 g; *S. minor* mean = 1.36 g, ll 1.02 g and ul 1.80 g; significant interaction, Table 2). Growth of shoots of *T. repens* was not significantly affected by the experimental manipulations (Table 2).

Soil nutrients and water

The amount of nitrate and ammonium in the soil at the end of the experiment did not differ between the low and moderate levels of nutrient availability, but was increased in soil of highly fertilized microcosms (nitrate $F_{2, 140} = 16.88$, $P < 0.001$; ammonium $F_{2, 140} = 15.50$, $P < 0.001$). Collembola increased soil nitrate and ammonium concentrations (nitrate $F_{1, 140} = 101.64$, $P < 0.001$; ammonium $F_{1, 140} = 23.80$, $P < 0.001$; Fig. 3). However, soil nutrients were not affected by aphids and plant composition (all $P > 0.1$).

At the end of the experiment, soil water concentration was lower with increasing nutrient availability (12.2% ± 0.22%, 11.9% ± 0.22%, and 10.7 ± 0.22 for the low, moderate, and high nutrient treatments [mean ± SE]; $F_{2, 140} = 12.14$, $P < 0.001$) and differed between plant species composition treatments ($F_{2, 140} = 5.03$, $P = 0.008$). These effects could be explained by differences in plant biomass between the treatments, and were no longer significant after inclusion of total plant biomass as a covariate in the analysis.

Collembola performance

During the experiment, Collembola density increased from 40 at the start of the experiment to an average of 603 individuals per microcosm at the end. Overall, the number of Collembola increased in the presence of leaf herbivory ($F_{1,68} = 5.30$, $P < 0.05$; Fig. 4A), whereas nutrient availability and plant composition had no effect (all $P > 0.1$). The effect of aphids was only significant in microcosms with high nutrient addition (significant interaction, $F_{2,68} = 3.47$, $P < 0.04$; Fig. 4A). Including plant biomass or soil water concentration as covariates in the analysis did not change these findings.

Aphid performance

The total number of aphids increased with nutrient availability (ANOVA, $F_{2,68} = 15.66$, $P < 0.001$) and Collembola ($F_{1,68} = 41.73$, $P < 0.001$, Fig. 4B), but did not respond to plant species composition ($F_{2,68} = 1.65$, P
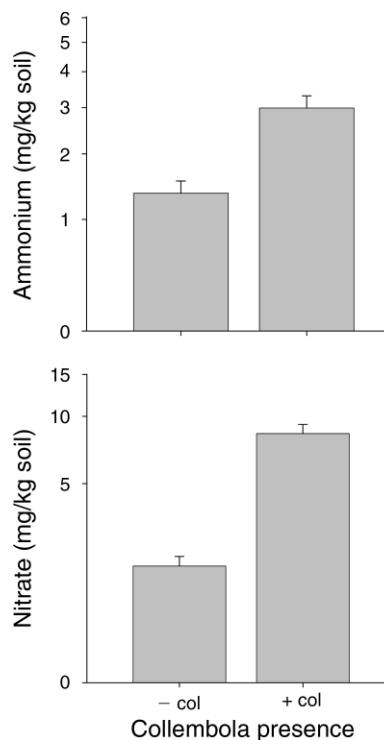

FIG. 3. Effects of Collembola (col) on the availability of ammonium and nitrate in the soil. Values are means + SE. Note that the *y*-axes are log scales.
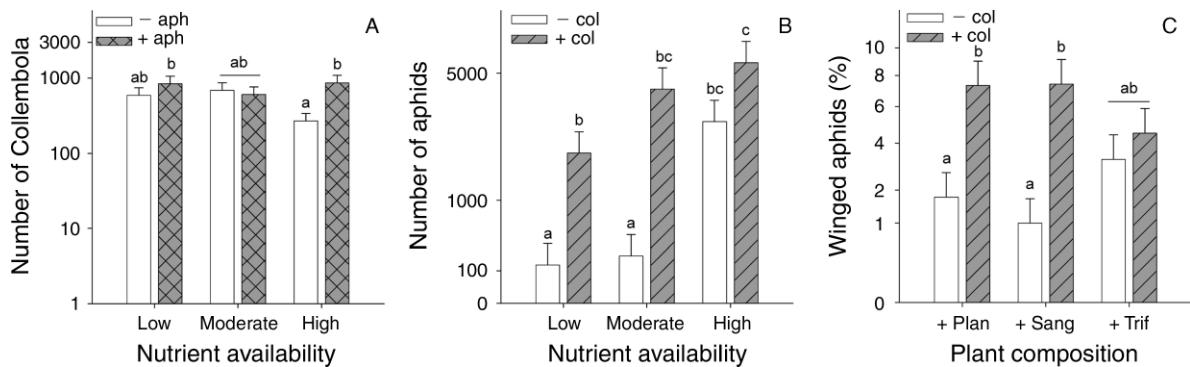
FIG. 4. (A) Effects of nutrient availability and aphids on the number of Collembola in the microcosms. (B) Effects of nutrient availability and Collembola on the number of aphids on *Poa annua*. (C) Effects of plant composition and Collembola on the percentage of winged aphids on *Poa annua*. Abbreviations are: col, Collembola; aph, aphids. Plant composition: *Poa annua* with *Plantago lanceolata* (+ Plan), *Sanguisorba minor* (+ Sang), or *Trifolium repens* (+ Trif). Values are means + SE. Significant differences between means are denoted with different letters above the bars following Tukey's hsd post hoc test ($P < 0.05$). For statistical analyses, see *Methods: Statistical analyses*.

> 0.1). The increase of aphid numbers with the activity of Collembola was most pronounced at low and moderate nutrient availability (Fig. 4B). In the absence of Collembola, aphid density increased in microcosms with high soil nutrient availability (significant interaction, $F_{2,68} = 3.18$, $P < 0.05$; Fig. 4B). Aphid numbers increased with grass shoot biomass ($r^2 = 0.39$, $P < 0.001$) as well as with nitrogen concentration ($r^2 = 0.20$, $P < 0.001$) and even slightly with shoot carbon concentration ($r^2 = 0.05$, $P < 0.04$). However, using element concentrations as covariates did not change the results. If biomass was fitted as a covariate, aphid numbers only increased in the presence of Collembola ($F_{1,67} = 48.65$, $P < 0.001$), whereas the effect of nutrient addition was no longer significant.

Presence of Collembola resulted in an up to 7.5-fold increase of the proportion of winged aphids ($F_{1,68} = 21.63$, $P < 0.001$; Fig. 4C). The proportion of winged aphids showed a weak positive correlation to nitrogen concentration in grass shoots ($r^2 = 0.06$, $P = 0.017$). We found no correlation with shoot biomass or carbon concentration in shoots of *P. annua* ($P > 0.1$). If nitrogen concentration was taken into account as a covariate, Collembola increased the proportion of winged aphids more strongly at low nutrient availability (significant interaction Collembola × nutrient availability, $F_{2,67} = 4.40$, $P = 0.016$).

DISCUSSION

In accordance with our hypotheses, nutrient availability and decomposers affected plant growth and herbivore performance in an interactive way. Furthermore, aphid herbivory in turn affected decomposers and this again depended on plant nutrient availability.

Plant performance

With the exception of *Trifolium repens*, nutrient addition increased plant biomass, indicating that plant growth was nutrient limited. Collembola in general

reduced root biomass, thereby changing resource allocation within the plant towards the shoots. Collembola-mediated reductions in root biomass have been observed in several other studies (Scheu et al. 1999, Kreuzer et al. 2004, Partsch et al. 2006). These results suggest that both decreased root and increased shoot biomass in decomposer treatments may reflect an increase in nutrient mobilization from fungi by feeding of the Collembola (Ineson et al. 1982, Filser 2002), and an enhanced plant nutrient uptake (Scheu et al. 1999, Gange 2000, Kreuzer et al. 2004, Lussenhop and BassiriRad 2005, Partsch et al. 2006). This further agrees with the increased concentration of mineralized nitrogen observed in the soil of decomposer-microcosms as well as the increased nitrogen concentration in shoots of the focal plant *Poa annua* due to Collembola activity. Increased plant growth due to Collembola may be also related to changes in the community composition of fungi and microorganism in the rhizosphere (Klironomos et al. 1999, Kreuzer et al. 2004, Tiunov and Scheu 2005). Furthermore, grazing by Collembola may stimulate mycorrhizal infection (Finlay 1985, Harris and Boerner 1990, Ek et al. 1994).

Our experiment also showed that effects of decomposers depended on plant species composition. Compared to assemblages of *P. annua* and either *Pl. lanceolata* or *S. minor*, assemblages with *T. repens* showed only a weak increase in shoot biomass in the presence of Collembola. The symbiosis with nitrogen fixing bacteria is advantageous for *T. repens*, particularly at a low nutrient availability (Høgh-Jensen and Schjoerring 1997, Munoz and Weaver 1999), resulting in higher shoot biomass in these assemblages even in the absence of decomposers. The lack of response of *T. repens* to an additional nutrient supply, either due to decomposer activity or experimental nutrient addition, contrasts those of Partsch et al. (2006), who showed that Collembola increased the biomass of the legume *Onobrychis viciifolia*. The results indicate that the

positive decomposer effects on shoot growth are due to a stimulation of nutrient uptake, which may explain why the decomposer effects decrease with increasing nutrient availability in the soil.

The reduction of *P. annua* biomass by aphids, especially at the highest level of nutrient availability, was caused by the increased reproduction of aphids (see *Aphid performance*). This effect could not be counteracted by compensatory growth of plants. The impact of herbivory on biomass as well as nitrogen concentrations in shoots of *P. annua* was stronger in the presence of Collembola. This indicates that the Collembola-mediated increase in aphid population growth (see *Aphid performance*) partly antagonizes the positive effects of decomposers on plant biomass and nutrient concentration in plant tissue of *P. annua*. Even if it has been shown before that decomposers increase the performance of aboveground herbivores (see *Aphid performance*), this is, to our knowledge, the first study to show a decomposer-modified top-down effect of leaf herbivores on plant biomass. In contrast to the separate effects of Collembola and aphids on plant growth and the interacting effects on each other's performance, the interacting effects of Collembola and aphids on the total plant biomass were not dependent on nutrient availability in this study.

Aphid performance

The considerable increase in aphid numbers during our experiment concurs with published results (Dixon 1971, Schädler et al. 2007*a*). Furthermore, the enhanced rate of reproduction of aphids with increasing nutrient availability is consistent with previous studies (Jansson and Smilowitz 1986, reviewed by Waring and Cobb 1992). By increasing the content of mineralized nitrogen in the soil and thereby stimulating growth and nutritional status of the host plant, Collembola affected population growth of the aphid *Rhopalosiphum padi* on *P. annua*. This positive effect may have been caused by the increased nitrogen concentration in shoots of *P. annua* (Lussenhop and BassiRad 1995, Bargett and Chan 1999, Partsch et al. 2006), since nitrogen is an important limiting factor for leaf herbivores (Dixon 1998, van Emden and Bashford 1969, Srivastava 1987). Similar to their effects on plant growth, the decomposer-mediated increase in numbers of aphids (by a factor of 15 to 20) was more pronounced in microcosms with low and moderate nutrient availability. In contrast to Schütz et al. (2008), Collembola positively affected aphid numbers even at high nutrient availability, which was still evident even after taking the effect of nitrogen in shoots into account. The activity of decomposers may further change the quality of nitrogen-based compounds in phloem sap and thereby affect aphid reproduction (Van Emden and Bashford 1969, Dixon 1998) independently from their effects on the nitrogen uptake by plants.

Decomposer activity, but not experimental nutrient addition, increased the formation of winged aphid morphs. Winged morph production has been discussed as a response to unfavorable environmental conditions (low host quality, high aphid densities; see Müller et al. [2001]). Since the positive impact of the decomposers on numbers of aphid offspring was stronger than that of experimentally enhanced nutrient availability, increased numbers of winged morphs are likely to be the consequence of crowding due to enhanced fecundity (Müller et al. 2001). Furthermore, Collembola- rather than nutrient-mediated changes in the quality of the phloem sap of *P. annua* may explain this phenomenon. Wing formation in aphids is increasingly discussed as the result of interactions with predators, pathogens and mutualistic ants (Müller et al. 2001), whereas any evidence for a similar role of decomposers is lacking until now.

Collembola performance

In contrast to the study of Schütz et al. (2008), experimental nutrient addition did not increase the number of Collembola in the microcosms. However, unlike in the study of Schütz et al. (2008), where the watering regime of the microcosms was adjusted to the water uptake by plants, we applied a constant water volume per pot. This resulted in a lower soil water content caused by a higher plant biomass at high nutrient availability, which in turn may have affected the Collembola (but see Sinka et al. 2007). Therefore, environmental factors such as moisture conditions and soil chemical parameters may have limited the Collembola population at higher levels of nutrient availability (Klironomos and Kendrick 1995, Hopkin 1997). This more closely resembles field conditions, since highly productive plant communities are more likely to suffer from shortage of water.

The positive effect of herbivores on Collembola at high nutrient availability is in accordance with Bardgett and Wardle (2003), who stated that such effects are more common in highly productive habitats mainly due to an increased carbon addition to soil and alleviation of carbon limitation of microflora. We could show that this effect was not due to herbivory-induced changes in plant biomass and, as a result, water content of the soil. Rather, aphids more likely changed the physiological responses in *P. annua* which resulted in changes in root exudation and carbon allocation (Sinka et al. 2007) or stimulated microbial biomass through honeydew excretion.

Conclusions

The results of our experiment showed that soil nutrient availability is crucial for understanding the consequences of above- and belowground trophic interactions for ecosystem functioning. Consequently, the effects of environmental variability on trophic interactions both above- and belowground as well as

the linkages between the two subsystems have to be integrated into models of community and ecosystem dynamics. We could demonstrate that the increased performance of plants and their associated herbivores due to decomposer activity is limited to systems with rather low availability of soil nutrients. In contrast, the performance of leaf herbivores is usually enhanced by increased nutritional status of their host plant. This results in a stronger top-down effect of leaf herbivores on the vegetation when nutrients are plentiful. Therefore, the relative importance of decomposers and herbivores as structuring forces for the dynamics of plant communities are likely to change along gradients of nutrient availability.

Consequently, by affecting each other's performance, the effects of decomposers and herbivores on plant performance interact. To our knowledge, this is the first study showing interacting effects of leaf herbivores and decomposers on the vegetation. Since aboveground herbivores may significantly affect the structure and productivity of plant communities, decomposers may play a crucial role in mediating these effects.

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