

Effects of decomposers and herbivores on plant performance and aboveground plant–insect interactions

Katja Poveda, Ingolf Steffan-Dewenter, Stefan Scheu and Teja Tscharnatke

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Most ecologists acknowledge that plants are subject to complex interactions between both below- and aboveground dwelling animals. However, these complex interactions are seldomly investigated simultaneously. In a factorial common garden experiment we tested single and combined effects of decomposers, root herbivores and leaf herbivores on the growth, flower visitation, and abundance of naturally colonizing aphids and parasitoids on wild mustard (*Sinapis arvensis*). We found that the individual presence of either root herbivores or decomposers resulted in increased aphid abundance, demonstrating that the same aboveground plant–insect interaction can be released by different belowground processes. Enhanced aphid densities caused higher numbers of parasitoids. Furthermore, decomposers increased plant growth and plant fitness (measured as the number of seeds produced), indicating that mustard may benefit from nutrients provided by decomposers, regardless whether plants are attacked by root herbivores or leaf herbivores, or both simultaneously. More flower visits were observed in plants attacked by root herbivores but without leaf herbivores than in plants with both herbivores, suggesting that root herbivory can modify flower attractivity to pollinators. Our results suggest that patterns in plant–insect interactions above the ground are not only affected by aboveground factors but also by a wealth of different belowground processes mediated by the plant.

K. Poveda, I. Steffan-Dewenter and T. Tscharnatke, *Agroecology*, Göttingen Univ., Waldweg 26, DE-37073 Göttingen, Germany (kpoveda@uaoe.gwdg.de). – S. Scheu, *Zoology*, Technische Univ. Darmstadt, Schnittspahnstraße 3, DE-64287 Darmstadt, Germany.

All terrestrial ecosystems are divided in a belowground and an aboveground subsystem. These subsystems are obligately dependent upon one another, since above the ground primary producers are the main source of organic carbon for the system, whereas below the ground organisms are in charge of the recycling of organic matter and the mineralization of the nutrients therein (Scheu and Setälä 2002, Wardle 2002). Therefore, in order to understand community and ecosystem-level processes it is necessary to study the interactions that occur within and between these subsystems. Most ecologists have investigated belowground and aboveground communities separately, leaving the “between

subsystems” interactions mostly unstudied (but see Bonkowski et al. 2001, van der Putten et al. 2001, Brown and Gange 2002). Studies on the interactions of ecological processes, such as decomposition, herbivory, parasitism and pollination, are needed to improve our knowledge on the role of plants as mediators between the belowground and the aboveground subsystems.

It is known that decomposers are responsible for the breakdown of organic matter and the release and cycling of nutrients (Haimi and Einbork 1992, Wardle 2002). The activity of decomposers often results in increased plant growth and plant nitrogen content (Scheu and Parkinson 1994, Bonkowski et al. 2000, 2001, Wardle

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2002) which in turn enhances plant herbivory (White 1993, Bonkowski et al. 2001).

Root herbivory is known to reduce plant growth and to increase mortality of plants (Brown and Gange 1990, Wardle 2002). Further, it may affect the flowering period, the number of flowers and the size of inflorescences (Nötzold et al. 1998, Masters et al. 2001), which could be expected to change attractiveness to flower visitors. The effect of root herbivores on aboveground herbivores is debated. One hypothesis predicts that root herbivory enhances aboveground herbivores. This is assumed to result from an accumulation of carbohydrates and nitrogen in shoots as a stress response of the plant to root herbivory (Gange and Brown 1989, Masters and Brown 1992, Masters et al. 1993, 2001). Another hypothesis suggests negative effects caused by the induction of secondary plant compounds which are stored in the foliage and act as deterrents to aboveground herbivores (Bezemer et al. 2002).

Foliar herbivory may affect plant fitness directly by reducing the photosynthetic area (Strauss 1991, Marquis 1992) and indirectly by altering patterns of pollinator visitation of damaged plants (Lehtilä and Strauss 1997, 1999, Strauss 1997, Mothershead and Marquis 2000). Seed production may be reduced substantially by herbivory, due to reduced resources available for flower, pollen or seed production or because of low pollination rates of damaged plants. Changes in the amount or chemistry of nectar (Hambäck 2001), the number or morphology of flowers (Karban and Strauss 1993, Strauss et al. 1996, Lehtilä and Strauss 1997, 1999) or the height of the flowers (Strauss 1997, Mothershead and Marquis 2000, Hambäck 2001) may reduce the attractiveness to pollinators. Studies on the combined effects of root herbivores, leaf herbivores and decomposers on plants are, however, lacking, and there is little information on the effects of these organisms on plant mutualists like pollinators.

Exposing *Sinapis arvensis* to wireworms, caterpillars and earthworms in a full factorial design we investigated how below- and aboveground plant–animal interactions affect both plant performance and the aboveground associated insect community. In a previous investigation we found that root and leaf herbivores modify plant growth and that root herbivores increase flower visitation (Poveda et al. 2003). Based on these results the present study investigates how decomposers and root herbivores and also leaf herbivores, separately and in combination, affect plant performance and aboveground antagonistic and mutualistic plant–insect interactions. We expected negative effects of root and leaf herbivores and positive effects of decomposers on plant growth, plant reproduction, flower visitation and the abundance of aphids and their parasitoids. We also expected that below- and aboveground herbivores in combination most strongly affect plant fitness and plant–insect

interactions, and that the detrimental effects of herbivores are counteracted by decomposers.

Methods

Experimental setup

The experiment was carried out on a fallow field in the vicinity of Göttingen (Lower Saxony, Germany) in 2002. Two-liter pots were lined inside with a gauze-bag (1 mm mesh) in order to prevent the escape of soil organisms in the pots and colonization by soil macrofauna from outside through the drain holes. This permitted to manipulate the larger decomposers and root herbivores but allowed colonization of the pots by meso- and microfauna. After lining the bottom of each pot was filled with 200 ml gravel to facilitate drainage. Pots were filled with defaunated soil, taken from a 10-year-old fallow located on a limestone plateau east of Göttingen. The soil was defaunated by freezing at -20°C for 3 days. This method has been shown to effectively eliminate macrofauna in the soil (Huhta et al. 1989). Five grams of litter material consisting mainly of grass leaves were placed on top of the soil. The litter material was collected on the field margin, dried at 60°C and cut into pieces of about 2 cm in length. The experiment was set up in a three factorial design. The effects of root herbivores (R), decomposers (D) and leaf herbivores (L) on plant growth and reproductive parameters of mustard (*Sinapis arvensis*) were investigated. The full complement of combinations was set up (Control, D, R, DR, L, DL, LR, DLR) with ten replicates each. Two earthworms of the species *Octolasion tyrtaeum* were added to each pot of the decomposer treatment. The density chosen (50 earthworms m^{-2}), is in the lower range of densities in the field ($9\text{--}239$ ind m^{-2} , Pizl 1999). Earthworms were weighed prior to placement in the pots (average fresh weight of the two individuals: 6.18 ± 0.8 g, mean \pm SE). Five wireworms (larvae of the click beetle *Agriotes* sp.) were added to each pot of the root herbivore treatments, which is equivalent to a density of ca 125 individuals m^{-2} (average fresh weight 0.4 ± 0.03 , mean \pm SE). Wireworms are patchily distributed in soil and may reach densities of up to several hundred per square meter (Poveda et al. 2003).

Seeds of *S. arvensis* from a regional wild population (provided by the Botanical Garden, Göttingen) were sown in the greenhouse on 29 April 2002. On May 20 young seedlings were transplanted into the experimental pots, to which the soil organisms had been added previously. The seedlings had developed four to six true leaves. One day after transplantation two third instar larvae of *Spodoptera littoralis* (obtained from Syngenta Corp. Protection Münchwilen AG) were put on the seedlings. The larvae were left on the plants until they had consumed ca 50% of the leaves, which took

approximately two days. Leaf herbivory was restricted to a short period early in the experiment to allow investigation of its effect on herbivores (aphids) attacking the plant later.

Any other subsequently produced leaves were left undamaged. On May 28 all pots were transferred in random order to the field. The pots were buried into the soil leaving only 3 cm of the upper margin above the soil surface. At periods of low precipitation the pots were watered with tap water.

Sampling and statistical analyses

The beginning and the end of the flowering period was recorded for each plant. When the plants began to flower the number of aborted flowers was counted. We considered aborted flowers as the flower buds that never opened.

Observations of flower-visiting insects were made during the flowering period from 14–20 June 2002. Each plant was observed for 45 min, divided in three observation periods of 15 min. These observation periods were distributed randomly on three different days between 10 AM and 4 PM. For each plant the number of open flowers was counted to compare plants with different numbers of flowers. In order to compare flower visitation rates we calculated the number of flower visits per open flower within a 15 min interval. Plants were naturally colonized by aphids during the experiment in the field. Each week (beginning on June 12) the aphids were identified and number of aphids on each plant was counted as well as the number of mummified aphids until plants started dying off (July 16). Mummies (i.e. parasitised aphids) were collected and stored in test tubes closed with cotton in order to let parasitoids hatch for further identification. Percent parasitism was calculated as the percent mummified aphids.

The experiment was finished when fruits turned yellow (July 2002). Individual plants were collected and oven dried for three days at 60°C to determine dry weight. While washing the roots, earthworms and wireworms were collected and counted. At the end of the experiment 83% of the earthworms and 90% of the

wireworms were present and no differences were found in the number of earthworms or wireworms between treatments ($p > 0.1$).

Number of fruits (=pods) of each plant was counted. Twenty fruits were randomly selected and seeds were counted and weighed. These data were used to calculate the number of seeds per plant. Data on plant biomass, shoot/root ratio, flowering period, total number of flowers and number of seeds per plant were analyzed using a multivariate analysis of variance (MANOVA). If significant, protected ANOVA's were performed to locate which of the dependent variables responded most to the factors studied (Scheiner and Gurevitch 2001). This procedure was preferred to Bonferroni corrections to avoid increasing the probability of type I errors (Legendre and Legendre 1998, Moran 2003). There were significantly more differences than expected by chance (Moran 2003; Table 1; the probability that 6 out of 35 possible tests are significant by chance is 0.0057 according to Bernoulli equation). Data on flower visitation, aphid abundance and parasitism rates of aphids were also analyzed by three factor analysis of variance. Differences between means were inspected using Tukey's honestly significant difference test. Since we were not interested in measuring differences in aphid numbers between weeks but in differences between treatments the data were standardized prior to ANOVA. For this the relative abundance of aphids was calculated by dividing aphid abundance per pot by the mean abundance of all pots in each week. From the relative abundance of aphids for each week the mean of all weeks was calculated and used for the ANOVA. Data on plant biomass, shoot/root ratio, number of flowers and seeds per plant and flower visitation rate were log transformed prior to ANOVA to adjust to normal distribution and to increase homogeneity of variance. Correlations between the number of aborted flowers and the length of the flowering period and between the number of visited flowers and the number of flowers were analyzed with Spearman's rank correlations. Statistical analyses were performed using Statistica 5 (StatSoft 1995).

Table 1. ANOVA table of F-values on the effect of decomposers (D), leaf herbivores (L) and root herbivores (R) on plant biomass, shoot/root relationship, number of flowers, flowering period and seeds per plant.

Treatment	df	Plant biomass	Shoot/root	Flowers	Flowering period	Seeds per plant
D	1, 72	8.44**	0.66	5.75*	3.93	12.17***
L	1, 72	2.518	2.25	1.12	34.17***	2.677
R	1, 72	4.83*	0.34	1.83	0.03	2.33
DL	1, 72	0.142	6.63*	0.33	1.13	0.6
DR	1, 72	2.52	0.87	3.5	0.18	3.04
LR	1, 72	0.57	0.005	1.58	0.82	0.69
DLR	1, 72	3.59	0.56	1.24	0.26	2.04

* $p < 0.05$; ** $p < 0.01$, *** $p < 0.001$.

Results

Plant performance

The plant growth parameters measured varied between plants with and without decomposers (MANOVA; $F_{5,68}=2.95$, $p=0.018$) and between plants with and without leaf herbivores (MANOVA; $F_{5,68}=10.70$, $p<0.0001$) but they didn't vary due to root herbivory or the interaction between the factors (MANOVA, $P>0.1$). Separate ANOVA's indicated that decomposers increased plant biomass (Fig. 1a), number of flowers (Fig. 1b) and number of seeds (Fig. 1c; Table 1). Decomposers also increased the shoot/root ratio, but only in absence of leaf herbivores (Fig. 1d). Plants subjected to leaf herbivory had a shorter flowering period than plants without leaf herbivory (Fig. 1e). Flowering period was negatively correlated with the number of aborted flowers at the beginning of the flowering period ($r = -0.54$, $n = 80$, $p < 0.001$).

Flower visitation

We observed 860 flower visitors. The most abundant species was the honeybee (*Apis mellifera*) with 531 visits. The second most important group was wasps with 169 visits. The remaining visitors were bumblebees (predominantly *Bombus pascuorum*), hover flies (predominantly *Eristalis tenax*) and other flies (Diptera). The number of flower visits increased with the number of flowers per plant ($r = 0.64$, $n = 80$, $p < 0.001$). There were more flower visits per open flower (i.e. the proportion of all flowers per plant that were visited during one observation period) in plants with root herbivores than without them but only when leaf herbivores were absent (Fig. 2a; Table 2).

Herbivores and parasitoids

Aphids on the plants were dominated by *Brevicoryne brassicae* (77% of all aphids present). Other species included *Lipaphis erysimi* (14.4%) and *Aphis* sp., *Myzus persicae* and *Macrosiphon euphorbiae* (8.6%). Plants which had been attacked by leaf herbivores at an early stage in their development had less aphids than plants without leaf herbivory pre-treatment (Table 2, Fig. 2b). Root herbivores and decomposers also affected the total number of aphids on the plants (Table 2). In treatments with only earthworms or with only root herbivores the number of aphids was increased compared to control plants (Fig. 2c). The number of parasitoids increased as the number of aphids on a plant increased ($r = 0.6739$, $n = 80$, $p < 0.001$) but there was no effect of herbivores or decomposers on the rate of parasitism of the aphids (Table 2).

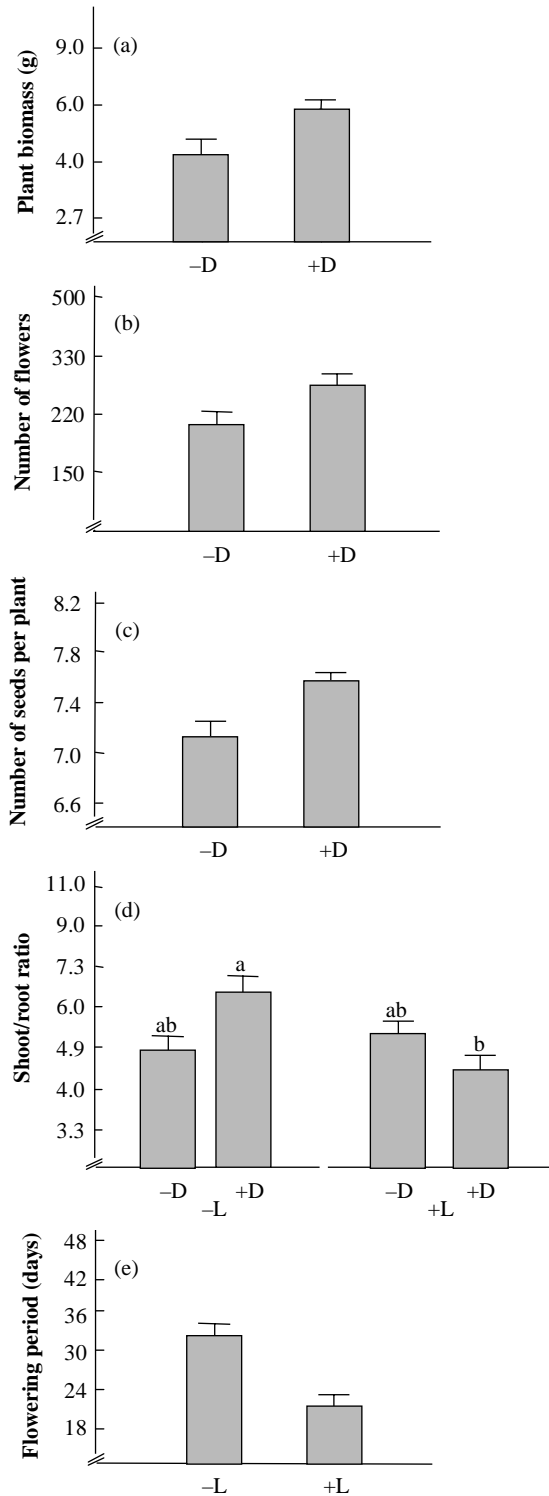


Fig. 1. Effects of decomposers (D), leaf herbivores (L) and root herbivores (R) on plant biomass (a), number of flowers (b), number of seeds per plant (c), shoot-root ratio (d) and flowering period (e) of *Sinapis arvensis* (mean \pm one SE). In (d) treatments with different letters are significantly different (Tukey's test, $p < 0.05$).

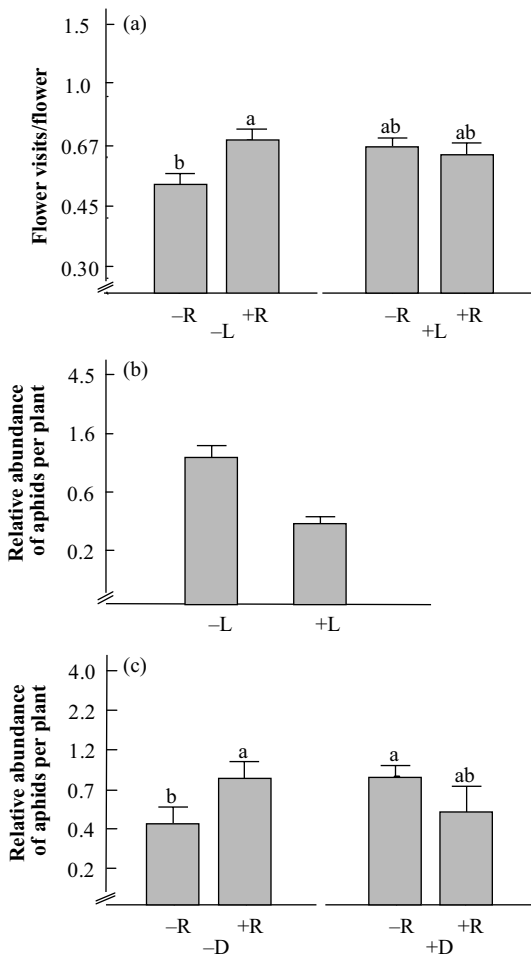


Fig. 2. Effects of decomposers (D), leaf herbivores (L) and root herbivores (R) on the flower visitation rate (a) and the number of aphids (b, c) (mean \pm one SE). In (a) and (c) treatments with different letters are significantly different (Tukey's test, $p < 0.05$).

Discussion

Although attention on complex food web interactions has increased in recent years, we are not aware of any study that has considered the relative importance and

Table 2. ANOVA table of F-values on the effect of decomposers (D), leaf herbivores (L) and root herbivores (R) on the flower visitation rate, the relative abundance of aphids and the number of parasitoids per aphid.

Treatment	df	Flower visits/ flower	Aphids	Parasitism (%)
D	1, 72	2.02	0.56	0.82
L	1, 72	0.95	37.99***	0.27
R	1, 72	2.54	0.31	0.15
DL	1, 72	0.02	0.21	2.84
DR	1, 72	0.21	5.83*	0.34
LR	1, 72	4.45*	0.23	2.99
DLR	1, 72	2.12	1.59	1.53

* $p < 0.05$; ** $p < 0.01$, *** $p < 0.001$.

combined effects of decomposers and above- and below-ground herbivores on the aboveground herbivore-parasitoid and plant-pollinator interactions. Having a standardized experimental approach, this study permitted new insights in the complex world of below-ground and aboveground plant-animal interactions, including important indirect effects of root herbivores on pollinators and also of decomposers and root and leaf herbivores on aphid performance (Fig. 3).

Plant performance

Plant biomass was enhanced by the presence of earthworms, regardless of the presence of herbivores (below- and aboveground). Presumably, earthworms increased the amount of nutrients in soil which subsequently was taken up by the plant leading to an increase in plant biomass, number of flowers and seed production. Earthworms are known to increase nutrient cycling in soil through bioturbation, acceleration of decomposition of organic materials and an increase in microbial activity (Haimi and Einbork 1992, Wardle 2002). The enhanced nutrient mineralization has been shown to increase plant nutrient uptake and subsequently the growth of plants (Brussaard 1999, Bonkowski et al. 2001).

In the present study earthworms also increased the shoot/root ratio but only in plants that were not attacked by leaf herbivores. This indicates that *S. arvensis* was able to increase the shoot biomass in the presence of earthworms only when there were no leaf herbivores. Most likely this was caused by an increase in nutrient supply to the plants. Similar changes in resource allocation by plants due to increased nutrient mobilization by earthworms were observed by Scheu and Parkinson (1994) and Alpehi et al. (1996). The lack of increase in the shoot/root ratio in presence of both decomposers and leaf herbivores suggests that nutrients mobilized by earthworms could not compensate the damage caused by leaf herbivores.

Although root herbivory is known to reduce plant growth and to increase the mortality of plants (Brown and Gange 1990, Wardle 2002) in the present study, as in our previous experiment (Poveda et al. 2003) wireworms did not affect plant biomass. Leaf herbivory caused a shortening of the flowering period as a consequence of early flower abortion. The latter was presumably caused by a reduction of photosynthetic tissue, as suggested previously (Poveda et al. 2003). Again, this early flower abortion and reduced flowering period did not affect female plant fitness.

Flower visitation

The rate of flowers visited was higher in plants with root herbivores but without leaf herbivores. This suggests that

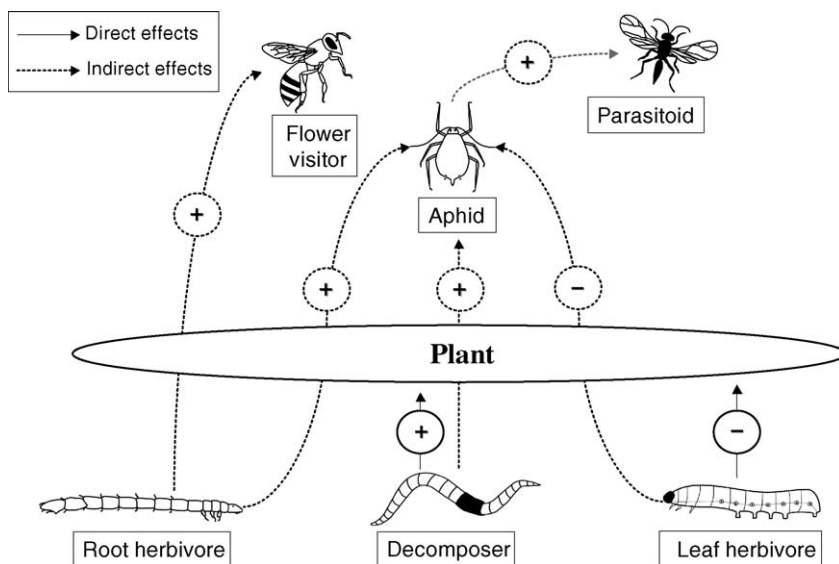


Fig. 3. Conceptual model of the direct and indirect effects of root herbivores, decomposers and leaf herbivores on *S. arvensis*, flower visitors, aphids and their parasitoids.

root herbivores increase plant attraction to flower visitors, as long as leaf herbivory did not counteract this effect. Low quantities of root herbivores have been shown to have a positive effect on flower visitors (Poveda et al. 2003). In the present experiment the density of wireworms was more than twice as high as in our previous study, but effects on flower visitation were similar. This suggests that root herbivores even at high density may stimulate the attractiveness of flowers to flower visitors. Masters et al. (1993) report that water stress, caused by root herbivory, leads to the accumulation of soluble amino acids and carbohydrates in the foliage. Possibly the carbohydrate concentration of nectar increased in presence of root herbivores augmenting the attractivity to flower visitors.

Aphid performance

Brevicoryne brassicae and *Lipaphis erysimi*, the most abundant species on *Sinapis arvensis*, are specialist herbivores on Brassicaceae (Blackman and Eastop 1984). They mainly colonized the flower stems of mustard. The stem forms a bottleneck for assimilates transported from the leaves to the buds, flowers and fruits (Stephenson 1981). Earthworms and root herbivores alone, but not in combination, increased the number of aphids. Aphids are highly susceptible to changes in host-plant quality (Way and Cammell 1970). Therefore the enhanced number of aphids on plants with earthworms or root herbivores may indicate an increased quality or quantity of assimilates transferred in the phloem. Nitrogen availability is one of the main factors limiting herbivore development (Mattson 1980, White 1993). Both decomposers and

root herbivores likely increased nitrogen availability to aphids. By stimulating nitrogen mineralization earthworms enhance the plant's nitrogen uptake and increase nitrogen concentration in plant tissues (Alpehi et al. 1996). By feeding on roots wireworms decrease the water uptake by the plant and consequently increased the nitrogen concentration in the phloem (Gange and Brown 1989, Masters and Brown 1992, Masters et al. 1993, 2001).

In our study root herbivory did not reduce the colonization of aphids in contrast to results of Bezemer et al. (2002) where root herbivores had a negative effect on foliar feeding herbivores, as a result of enhanced concentration of secondary plant compounds in the foliage. Since *S. arvensis* is a Brassicaceae, known for its glucosinolate content, the defense of *S. arvensis* against root herbivores may have been associated with an increase in glucosinolate concentrations. The reduced aphid colonization on plants with leaf herbivores suggest that the production of secondary plant compounds in *S. arvensis* may have been increased in response to leaf herbivory but not to root herbivory, although both below- and aboveground herbivores can induce the production of secondary compounds (reviewed by van Dam et al. 2003).

Reduced colonization of aphids on plants damaged by leaf herbivores might also have been caused by the delayed flowering of the plants affected by leaf herbivory. Since the inflorescence stem, where aphids feed, developed later on plants damaged by leaf herbivory, they could have been less attractive for colonizing aphids.

Herbivores in our study did not directly affect the third trophic level, aphid parasitism, which is concordant with the study of Masters et al. (2001). The number

of parasitized aphids only depended on the number of aphids per plant, the response of parasitoids therefore was indirect and density dependent.

Results of this experiment documented that below-ground organisms have much more effects on above-ground processes than assumed previously. The findings (i) that root herbivory affects pollinators and (ii) that aphids respond equally to decomposers and root herbivores add to existing knowledge on indirect effects of belowground processes on aboveground plant–animal interactions. Further studies and “in situ” experiments are necessary to evaluate the importance of these interactions in the field. Although relatively little experimental work has been done, the indirect interactions shown in this study are in line with mechanisms described in other investigations (Gange and Brown 1989, Masters et al. 1993, 2001, Alpehi et al. 1996) suggesting that the interactions found in the present study are significant drivers of plant–animal interactions above the ground in a variety of ecosystems.

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