

Belowground effects of organic and conventional farming on aboveground plant–herbivore and plant–pathogen interactions

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Abstract

Soil organisms may significantly affect the aboveground system. However, the influence of farming practices in modifying the effects of soil organisms on aboveground systems is poorly understood. The aim of our study was to investigate: (1) How important are soil organisms for plant growth and the development of herbivores and pathogens above the ground? (2) How do agricultural management practices affect interactions between soil organisms, plants and their aboveground herbivores and pathogens? To answer these questions we investigated the effect of experimental defaunation of soils from organic versus conventional farms on growth of wheat, abundance of aphids and infection of wheat by *Septoria* fungi. Plant biomass in soil from conventional farms exceeded that of soils from organic farms, presumably due to the higher nutrient input in the conventional farming system. Soil defaunation likely mobilized nutrients that increased plant growth. Aphid abundance and *Septoria* infection was reduced by defaunation but only in organic soils. This suggests that soil organisms in organic farming systems are more important for aphid performance and the infection rate by *Septoria* than in conventional systems. Hence, changes in the soil animal food web caused by farming practice feed back on aboveground organisms, and this appears to be more pronounced in organic farming systems. Further, the results indicate that soil organisms may modify higher trophic levels (aphid and pathogen infection) without significantly affecting lower trophic levels (plant growth).

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1. Introduction

Terrestrial ecosystems have a belowground and an aboveground subsystem. These subsystems depend on each other, since above the ground primary producers are the main source of organic carbon for the system, whereas below the ground soil organisms are responsible for the breakdown and recycling of organic matter and the mineralization of the nutrients therein (Scheu and Setälä, 2002; Wardle, 2002; Porazinska et al., 2003). To understand community and ecosystem level processes it is necessary to study the interactions within and between these subsystems. However,

most ecologists have investigated belowground and aboveground communities separately, leaving the interactions between the subsystems unstudied (but see Wardle et al., 1999; Wardle, 2002; Bonkowski et al., 2001; Masters et al., 2001; Van der Putten et al., 2001; Brown and Gange, 2002).

Current agricultural practices include the loss or degradation of non-crop habitats, the removal of weeds from within and around crops, enlargement of field sizes, tillage operations of varying degrees of intensity, and the use of chemicals to control pests and weeds in order to increase crop yield (reviewed by Gurr et al., 2003). These practices have caused serious ecological problems such as water contamination, habitat degradation and biodiversity loss (Matson et al., 1997; Krebs et al., 1999; Tilman et al., 2002), also affecting ecological functions such as pollination and

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biological control (Kruess and Tschardt, 1994, 2000; Matthies et al., 1995; Didham et al., 1996). In the belief that low intensity farming systems are beneficial for the agricultural environment, the European Union is supporting organic farming systems as an alternative to conventional agriculture (EU, 2002). In some European countries up to 8% of the agricultural area is managed organically (Mäder et al., 2002). Organic farming systems have a lower nutrient and pesticide input and an improved biological activity and biodiversity (Mäder et al., 2002; Hole et al., 2005).

Although there are several studies showing how below-ground biota affect aboveground organisms (Gange and Brown, 1989; Masters et al., 1993, 2001; Masters, 1995; Masters and Brown, 1997; Bezemer et al., 2002; Poveda et al., 2003, in press), studies comparing the importance of soil organisms in soils from different farming systems are missing. In order to study the importance of the soil biota on plant growth and the development of higher trophic levels and to analyze how farming systems affect the interactions between belowground and aboveground organisms we designed a replicated field experiment using wheat plants as model system. We investigated the effect of experimental defaunation in soils from organic farms and conventional farms on the growth of wheat plants and the performance of aphids and fungi on them. Two main questions were addressed: (1) How important are soil organisms for plant growth and the development of herbivores and fungi on these plants? and (2) How does the agricultural management practice of the soil affect interactions between soil organisms, plants and their aboveground herbivores and pathogens?

Our expectations were that soil organisms would increase plant growth in both soil types. However, since soils from the conventionally managed farms receive an increased input of fertilizers we expected that soil organisms would be more important for plant growth in soils from organic farms, and that this would also be reflected on the second trophic level, i.e. in the infestation rate of pathogens and herbivores.

2. Materials and methods

2.1. Experimental set-up

The experiment was carried out in the vicinity of Göttingen in the summer of 2003. Effects of farming practice (conventional versus organic) and the presence or absence of soil organisms (defaunated versus control soil) on wheat growth, aphid development and *Septoria* spp. infection were investigated in five landscape sectors. The landscape sectors were separated by 17.27 ± 8.26 km (mean \pm S.D.). They were chosen to represent the regional landscape and used as blocks. In the centre of each landscape sector, we selected one conventionally managed winter wheat field. In the middle of these conventional fields a plot of 700 m² (20 m \times 35 m) not treated with insecticides was established, where the experiment took place. Nearby we

selected an organically farmed winter wheat field from which soil samples were taken. From each field (five conventionally farmed and five organically farmed) 200 L of soil were collected and taken in plastic bags to a greenhouse. Half of the soil (100 L) were defaunated by freezing at -20 °C for 3 days which significantly reduces the number of soil microarthropods and annelids (Huhta et al., 1989). The soil was put into 10 L pots that were covered at the bottom with a 200 μ m mesh to prevent colonization by soil meso- and macro-fauna. In each pot 80 wheat (*Triticum aestivum*) seeds were sown on April 30th 2003. After germinating, the wheat plants grew in the greenhouse until May 23rd, when pots were set out in the fields. The experiment was set up in a randomized complete two factorial design with the factors farming system (soil from organic farming system versus soil from conventional farming system) and defaunation treatment (defaunated versus control soil). The full complement of combinations was set up (defaunated organic, control organic, defaunated conventional and control conventional) with five replicates per treatment (soils from five different sites) in each landscape sector. Plants were left to be naturally colonized by aphids and infected by *Septoria* (mainly *S. tritici*) fungi during the experiment. Starting on June 10 2003, the aphids were identified and the number of aphids on 25 plants per pot was counted each week. The percentage infection of *Septoria* fungi was estimated by relating the amount of stems and leaves infected by *Septoria* to the total amount of stems and leaves in 25 plants in each pot. These measurements were repeated each week during 6 weeks, until the wheat was harvested on July 17 2002. Plants were collected and oven dried for 3 days at 60 °C to determine dry weight of roots, shoots and ears. The number of ears per pot was counted.

2.2. Statistics

To analyze the effects of defaunation and soil farming practice on plant growth we used a multiple analysis of variance (MANOVA) with farming practice and defaunation as categorical variables and the landscape sector as block. When 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 8 out of 15 possible tests are significant by chance is 0.175×10^{-6} according to the Bernoulli equation). Differences between means were inspected using Tukey's honestly significant difference test. Data on aphid abundance was cumulated for all weeks and the number of aphids per unit plant biomass was calculated by dividing the number of aphids per pot by the total biomass of the plants. This was done to correct for the differences in aphid abundance due to differences in plant biomass. Data

Table 1

Effects of defaunation and farming practice (conventional vs. organic) on the total biomass, shoot mass, root mass, ear mass and number of ears

	Total mass	Shoot mass	Root mass	Ear mass	Number of ears
Defaunation	$F_{1, 93} = 11.85$, $p < 0.001$	$F_{1, 93} = 5.21$, $p = 0.02$	$F_{1, 94} = 10.58$, $p = 0.0016$	$F_{1, 93} = 20.13$, $p < 0.0001$	$F_{1, 94} = 4.63$, $p = 0.034$
Farming practice	$F_{1, 93} = 6.35$, $p = 0.013$	$F_{1, 93} = 8.92$, $p = 0.003$	Not significant	$F_{1, 93} = 7.63$, $p = 0.007$	Not significant

The landscape sector was used as block. F and p -values (after model simplification) are shown.

on plant biomass were square root transformed, while data on the total number of aphids per biomass and on the percent damage by *Septoria* were log-transformed prior to the analysis to adjust to normal distribution and to increase homogeneity of variance. Correlations between the plant biomass and the number of aphids, as well as between the plant biomass and the percentage of *Septoria* infection were analyzed with Spearman's rank correlations. Statistical analyses were performed using Statistica 6.1 (StatSoft Inc., 2003) and R (2003).

3. Results

3.1. Plant performance

Plant growth parameters measured varied between plants grown in defaunated versus control soil (MANOVA; $F_{5, 88} = 5.78$, $p = 0.0001$) and between plants grown in soil from conventional versus organic fields (MANOVA; $F_{5, 88} = 3.99$, $p = 0.002$); there was no significant interaction between these factors (MANOVA, $p > 0.1$). Separate ANOVAs indicated that total plant biomass was affected by both the farming practice and the defaunation treatment (Table 1). Total biomass of plants grown in soil from conventional fields exceeded that of plants grown in soil from organic fields (Fig. 1a). This was true for the biomass of shoots and ears but not for that of roots (Table 1, Fig. 1a). Biomass of plants grown in defaunated soil exceeded that of plants grown in control soil and this was true for shoots, ears, roots and the number of ears per pot (Table 1, Fig. 1b).

3.2. Aphid and pathogen performance

In total we counted 33 985 aphids on the wheat plants. The most common species was *Sitobion avenae*, with 93.47% of the individuals followed by *Rhopalosiphum padi* with 5.65% of the individuals. *Metopolophium dirhodum* and two other species comprised each less than 0.5% of the individuals. Soil defaunation, but also the interaction between farming practice and defaunation, significantly affected the number of aphids per gram of plant biomass and the percentage of infection by *Septoria* (Table 2). The number of aphids per unit plant biomass in control soil exceeded that of defaunated soil but this was only true for organic soils and not for conventional soils (Fig. 2a). Defaunation of organic soil also reduced the infection of wheat by *Septoria*, but again this effect only

occurred in organic soils (Fig. 2b). There was no significant correlation between the number of aphids and plant biomass per pot ($r = 0.159$, $p = 0.113$), nor between the percentage of *Septoria* infection and plant biomass ($r = 0.0029$, $p = 0.977$).

4. Discussion

4.1. Plant performance

Plants biomass was higher in soils from conventional fields than in soils from organic fields. Soil defaunation increased plant biomass, irrespective of the farming system.

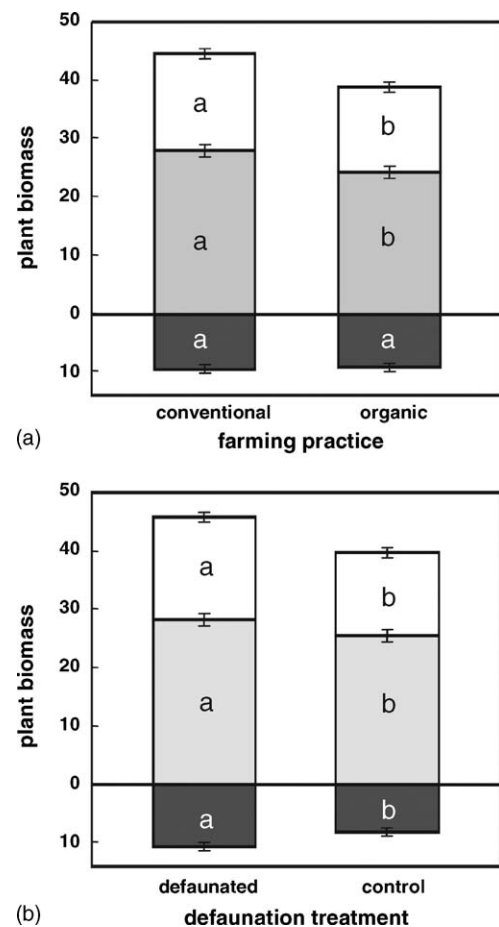


Fig. 1. Effects of (a) conventional vs. organic farming system and (b) defaunated soil vs. control soils on the biomass of wheat plants (■ roots, ■ shoots □ and ears) at the end of the experiment. Means \pm 1 S.E. are presented. Different letters indicate significant differences ($p < 0.05$).

Table 2

Effects of defaunation and farming practice (conventional vs. organic) on the number of aphids per gram dry plant biomass and the maximal percentage of *Septoria* infection

	d.f.	Aphids/biomass	%Septoria
Defaunation	1, 92	9.75**	5.89*
Farming practice	1, 92	0.07	0.31
Defaunation × farming practice	1, 92	6.26*	5.99*

The landscape sector was used as block. *F*-value and significance are shown.

* $p < 0.05$.

** $p < 0.01$.

In contrast, the number of aphids on wheat and the infection of wheat by *Septoria* were increased by defaunation in organic soil. This indicates that effects of soil organisms on plant–herbivore and plant–pathogen interactions depend on the farming system.

The higher plant biomass in the defaunated treatment compared to the control soil presumably was due to nutrients released by the defaunation procedure. Freezing is known to reduce the number of microarthropods and

nematodes in soil and to increase the amount of mineral nitrogen, in particular that of ammonium (Huhta et al., 1989). Ammonium is easily absorbed by plants and results in increased plant growth. Similarly, differences in the growth of plants between organic and conventional farming systems might have been due to higher nutrient input (N, P, K) in the conventional system (Mäder et al., 2002). When comparing the nutrient content of 13 organic farms with 13 conventional farms in the year 2003 in the surroundings of Göttingen (of which five overlapped with the present study) it has been shown that the amount of P is significantly increased in the conventional farming system, other nutrients being not significantly affected (Gabriel et al., unpublished data). Organic farming systems typically receive less nutrient input resulting in reduced crop yield in comparison to conventional farms (Mäder et al., 2002).

4.2. Aphid and pathogen performance

Soil defaunation did not affect the number of aphids per plant biomass in soil of the conventional farming systems while it reduced aphid numbers on plants growing in soil of organic farming systems. Because aphid reproduction depends on the nutritional quality of the host plant (Honek, 1991) the decrease in the number of aphids likely were caused by lower nutritional quality of the plants, mainly that of ears, since this is where *S. avenae* preferentially feeds on (Honek, 1991). Soil organisms are known to affect the development of above ground organisms, such as herbivores, through indirect effects mediated by the plant (Scheu, 2001; Bardgett and Wardle, 2003; Wardle et al., 2004). The decomposition of organic matter and related processes, such as mineralization of nutrients, are regulated by the decomposer food web (Wardle et al., 1999; Ruess et al., 2004). Therefore, the presence of decomposer invertebrates in the soil may beneficially affect the reproduction of aphids, as has been shown previously (Scheu et al., 1999; Bonkowski et al., 2001; Wurst and Jones, 2003). In our study soil defaunation was assumed to result in reduced decomposition processes. In fact, defaunation only caused a reduction in the aphid number in the organic soils but not in the conventionally managed soils suggesting that organically managed soils exhibit greater biological activity than conventionally managed soils, as has been shown previously (Mäder et al., 2002; Fließbach and Mäder, 2000). Therefore, differences in the number of aphids presumably resulted from both an increased activity of soil organisms in organic soils and a higher nutrient input in conventional soils. It is important to realize that these results cannot be extrapolated easily to real agricultural environments. Although the results suggest that wheat plants in organic fields are more heavily attacked by aphids, it has to be considered that the plants were uniformly exposed in conventional fields. As has been shown by Mäder et al. (2002) and Hole et al. (2005) aboveground biodiversity and also predator abundance is increased by organic farming.

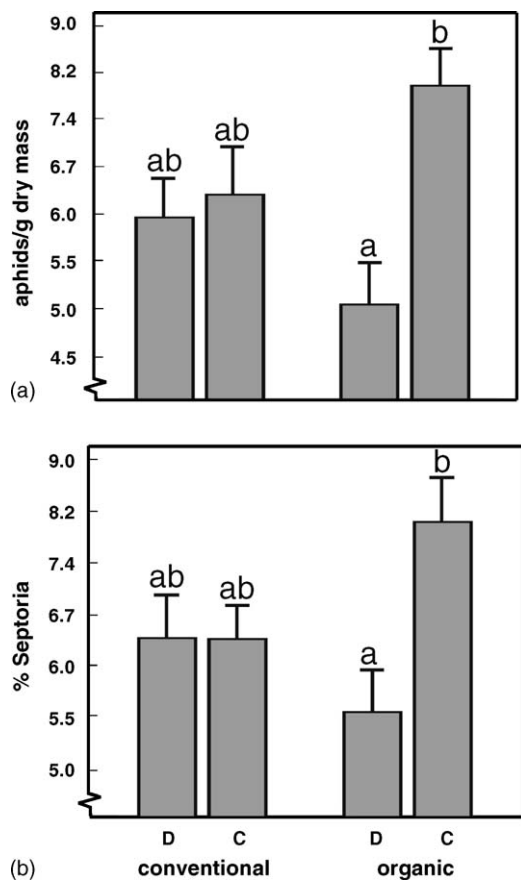


Fig. 2. Effects of defaunation treatment (D: defaunated soil, C: control soil) and farming practice (conventional vs. organic) on (a) the number of aphids per gram dry weight of total plant biomass and (b) the maximal percentage of *Septoria* infected stems and leaves. Means \pm 1 S.E. are presented. Bars with different letters are significantly different (Tukey's test, $p < 0.05$).

This suggests that although aphid nutrition may be increased in organically managed fields predators may more vigorously control aphid populations.

The results from our study suggest that the attack of wheat by plant pathogens, such as *Septoria* fungi, is increased on control organically managed farming systems in comparison to defaunated organic soils. Presumably, soil nutrients mobilized due to the activity of decomposer invertebrates facilitated the attack of wheat by *Septoria* and aphids in organic soils, likely because of higher decomposer activity in organic soil than in conventional soil. The fact that soil invertebrates facilitated both the infestation of wheat with aphids and *Septoria* fungi in organic soils without increasing wheat biomass suggests that soil organisms may enhance the food quality of plants for herbivores and pathogens without affecting plant growth.

5. Conclusions

Contrary to our expectations soil from different farming systems and soil defaunation did not consistently affect plant growth and plant attack by herbivores and pathogens. Plant growth appeared to depend on nutrient resources already in the soil at the experimental set up which was higher in conventional as compared to organic soils and in defaunated soils compared to control soils. In contrast, herbivores and pathogens relied on nutrients mobilized due to the activity of soil organisms in the organic soils during the course of the experiment. The results also suggest that soil organisms may increase the susceptibility of plants for attack by herbivores and pathogens without increasing plant biomass production. The effect of soil organisms therefore may propagate into higher trophic levels above the ground without visible effects on the basis of the aboveground food web, the plant. Improvement of biological activity and biodiversity below-ground therefore likely results in a strengthening of food web interactions above the ground.

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