

# The impact of soil organism composition and activated carbon on grass-legume competition

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**Abstract** Belowground mechanisms involved in plant competition are still poorly understood. Since plant species are differently affected by soil organisms, changes in soil community composition might affect interspecific competition with consequences for plant community structure. We studied whether soil community composition affects competition between the grass *Holcus lanatus* L. and the legume *Lotus corniculatus* L. We established three different soil communities by adding no soil organisms (control), microorganisms <30 µm, and a soil suspension including microorganisms >30 µm, AMF and nematodes to gamma-sterilized soil. Nodulation and aboveground biomass of *Lotus* was decreased in the sterilized control soil and in the presence of *Holcus*. Contrastingly, the grass grew better in the presence of the legume than in monoculture and was not affected

by soil community composition. Legume monocultures tended to produce the greatest aboveground biomass of the plant combinations when soil microorganisms were present, while the root biomass in legume monocultures was the lowest. Then, in a second experiment, we used natural (not sterilized) soil and added activated carbon to test whether the reduced nodulation of *Lotus* in interspecific competition is caused by allelopathic compounds of *Holcus*. In the natural soil, nodulation and flowering of *Lotus* was reduced, but the aboveground biomass was not affected by the competition with *Holcus*. Contrary to our expectations, activated carbon had a strong negative effect on the nodulation, growth and flowering of *Lotus* and shifted the interspecific competition in favour of *Holcus*. Probably, activated carbon impeded the nodulation by disrupting the communication between the legume and N<sub>2</sub>-fixing bacteria. We suggest that interruption of plant-microbe communications by activated carbon might be widespread and will confound interpretations on the role of allelopathy. Generally, we observed that the symbiosis of the legume with N<sub>2</sub>-fixing bacteria plays a crucial role in the grass-legume competition. When the symbiosis was deterred, the legume was outcompeted by the grass.

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Nodules · Plant competition

## Introduction

Plants compete for limited resources in soil. However, due to the inaccessibility of soils, the mechanisms of belowground plant competition are often poorly understood. Complex interactions between plant roots, involving the exudation of allelopathic compounds, and plant species-specific interactions with soil organisms might mediate the outcome of the competition. The present study investigates the role of belowground biotic interactions in a grass-legume competition. In a first experiment, we ask whether different soil community compositions change the grass-legume competition. A second experiment addresses potential mechanisms of the competitive superiority of the grass.

By changing soil nutrient availability or selectively feeding on roots, soil organisms can alter interspecific plant competition. Plant competition is, for example, changed by soil microorganisms such as arbuscular mycorrhizal fungi (AMF; Fitter 1977; Watkinson and Freckleton 1997; van der Heijden et al. 2003), rhizobia (Butler 1988; Turkington et al. 1988), pathogens (van der Putten and Peters 1997; Ridenour and Callaway 2003), and plant-feeding nematodes (Chen et al. 1995; Pantone 1995; Verschoor et al. 2002). However, little is known about how soil community composition and biodiversity affect plant competition and community structure (Watkinson 1998; Bradford et al. 2002; Wardle et al. 2004; Bonkowski and Roy 2005). In soil communities containing mainly bacteria, legumes might profit from the presence of N<sub>2</sub>-fixing rhizobia (van der Heijden et al. 2006). Nonetheless, in more complex soil communities, interspecific plant competition might be changed by soil organisms such as AMF (Crush 1974; Trannin et al. 2000) and root-feeding nematodes (Chen et al. 1995). In a greenhouse experiment, we manipulated soil community composition and investigated the impact on monocultures and mixtures of the grass *Holcus lanatus* and the legume *Lotus corniculatus*, which naturally co-occur in later stages of secondary vegetation succession (van der Putten et al. 2000). We hypothesized that the competitive ability of *Holcus* decreases with increasing soil community complexity, since *Lotus* benefits from soil organisms such as rhizobia (van der Heijden et al. 2006) and AMF (Trannin et al. 2000; Chalk et al. 2006), while *Holcus* might be suppressed by plant-feeding nematodes (Verschoor et al. 2002).

Although a lot of studies have been done on grass-legume competition, the mechanisms why the grass is often outcompeting the legume are not clear. Competition with grasses can either suppress N<sub>2</sub> fixation of legumes or, if soil N concentrations are inhibitory to N<sub>2</sub> fixation, lead to higher proportion of N<sub>2</sub> fixed by the legume because of a depletion of soil N by the grasses (Butler 1988). Thus, the role of the symbiosis between N<sub>2</sub>-fixing bacteria and legumes in the grass-legume competition remains unclear. In our experiment, we observed that *Holcus* suppresses *Lotus* and its capacity to form nodules, irrespective of the soil community composition. To investigate the mechanisms of the competitive superiority of *Holcus*, we conducted an experiment with and without activated carbon which adsorbs potential allelopathic compounds (Inderjit and Callaway 2003) to test whether root exudates of *Holcus* impede the formation of nodules of *Lotus*. Additionally, root growth of the plant species was separately analysed to estimate their belowground competitive abilities. Plants exude soluble substances from their roots which can change their own rhizosphere community (Grayston et al. 1998; Kowalchuk et al. 2002; Marschner et al. 2004; Bais et al. 2004). However, root exudates can also influence plant competition directly by inhibiting root growth of neighbouring plants (Mahall and Callaway 1992) or indirectly by affecting the microbial community of neighbouring plants (Christie et al. 1974, 1978). In the case of grass-legume competition, grasses were reported to indirectly influence legume performance by affecting soil microorganisms (Turkington et al. 1988). However, the mechanisms of this indirect plant competition mediated by soil microorganisms remained largely unexplored. Since some evidence exists that plants can indirectly suppress legumes by exuding substances from the roots that deter nodulation (Rice 1968), we hypothesized that the reduction in nodulation and growth of *Lotus* in presence of *Holcus* will be alleviated in presence of activated carbon.

## Materials and methods

Seeds of *Holcus lanatus* L. and *Lotus corniculatus* L. (Conrad Appel, Darmstadt, Germany) were sown on wet paper in Petri dishes and placed in the greenhouse (16 h light, 20°C/25°C night/day temperature). Germinated plants were transplanted into seedling trays

filled with the gamma-sterilized (25 kGray) experimental soil one week after sowing. A loamy, sandy mineral soil from Mossel (Planken Wambuis, The Netherlands;  $N=0.13\%$ ,  $C=2.1\%$ ,  $C/N=16.7$ ) was used for the experiments.

#### Soil community composition

A total of 54 pots (11.5 cm height, 13 cm diameter) filled with 800 g gamma-sterilized (25 kGray) experimental soil were placed in a greenhouse with 16 h light and 20°C/25°C night/day temperature. Seedlings were planted from the seedling trays, where they had been grown for around 3 weeks, into the microcosms (day 1 of the experiment). Each pot received either two individual plants of *Holcus* or *Lotus* (monocultures) or one individual of each of the plant species together (mixture). To manipulate the soil community composition, different soil suspensions were prepared. First, we suspended 500 g of the non-sterilized experimental soil in 2 l water. Then, a third of each of the three plant combinations ( $N=18$ ) received 50 ml of this original soil suspension, another third received 50 ml of the same suspension sieved through a sieve (to filter out soil organisms  $> 30 \mu\text{m}$  such as AMF and nematodes), and the rest of the pots received the same amount of demineralised water. In this way we established three treatments with different soil community composition: “sterile”—no soil organisms added, “microorganisms”—microorganisms  $<30 \mu\text{m}$  added, “microorganisms + AMF + nematodes”—soil suspension including microorganisms  $>30 \mu\text{m}$ , AMF and nematodes added. Note that the “sterile” treatment does not remain sterile because of unavoidable microbial contamination during the course of the experiment, and that other soil organisms such as mites might have been present in the original soil suspension. Generally, the abundance of soil organisms in re-inoculated sterilized soil is lower than in natural, not sterilized soil. To assess the nematode community added with the original soil suspension, nematodes were extracted by decanting (Brinkman et al. 2004), determined and counted under a microscope (magnification  $10\times 20$ ). On average 200 nematodes per pot were added with the unfiltered soil suspension consisting of 36% plant feeders, 38% bacterial feeders, 2% fungal feeders and 24% omnivores.

In week 14 the plants were harvested and the inflorescences of *Lotus* were counted. After root

washing, the nodules of *Lotus* main roots were counted. The shoot and root biomass were dried in an oven at 70°C until constant weight.

#### Activated carbon

A total of 108 pots (11.5 cm height, 13 cm diameter) filled with 900 g non-sterilized experimental soil were placed in a greenhouse with 16 h light and 20°C/25°C night/day temperature. Half the pots ( $N=54$ ) received 9 g (approximately 3% by volume) activated carbon (Merck, Darmstadt, Germany) mixed homogeneously into the soil, the other half did not receive activated carbon. Seedlings were planted from the seedling trays where they had been growing for around 2 weeks into the microcosms (day 1 of the experiment). The pots were planted with either two individual plants of *Holcus* or *Lotus* (monocultures) or one individual of each of the plant species together (mixture). Three harvests (in week 3, 7 and 10) were conducted with the intent to be able to separate the roots of the individual plants and observe different stages of the belowground competition.

In week 3, a third of the pots of each treatment was harvested ( $N=36$ ). The root systems of the two individual plants within a pot were carefully separated and scanned with WinRHIZO (Regent Instruments Inc., Sainte-Foy, Canada). The nodules of *Lotus* were counted using a binocular. The shoots and roots of the plant individuals were dried in an oven at 70°C. In weeks 7 and 10, the second and third harvests were performed. The root systems of the individual plants could not be separated anymore. The nodules of *Lotus* were counted using a binocular. The shoots of the plant individuals and the total roots per pot (combined of the two individuals) were dried in an oven at 70°C. During the course of the experiment, the inflorescences of *Lotus* were counted.

#### Statistical analyses

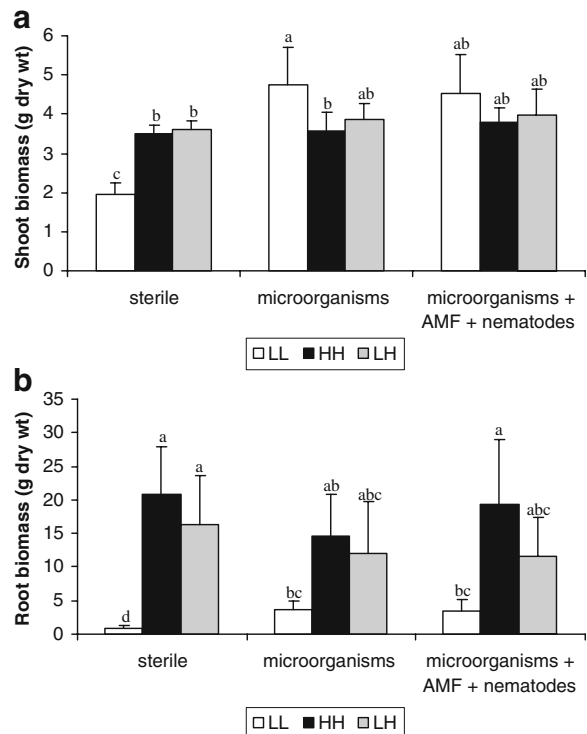
Data were analysed by factorial analyses of variance (ANOVA) in a general linear model (GLM, Statistica 6.0, Statsoft). For the first experiment the explanatory variables were “plant combination” and “soil community composition”. For the second experiment the biomass data of the three harvests were analysed separately with the explanatory variables “plant species”, “plant combination” and “activated carbon”.

The data were tested for normality (Kolmogorov–Smirnov one-sample test) and homogeneity of variances (Levene test) and log-transformed if necessary. When focusing on the plant species, the mean performance of the two individuals in monoculture was compared to the performance of the individual of the same plant species in interspecific competition. For the number of flowers and nodules of *Lotus* a repeated measurement ANOVA (RANOVA) was performed with the factors “plant combination”, “activated carbon” and the within subjects factor “time”. In the figures, different Tukey HSD letters indicate significant differences ( $P < 0.05$ ) between the individual means. Note, however, that results and their interpretation are based on the ANOVA analyses which tests combined means (main factors) and interactions.

## Results

### Soil community composition

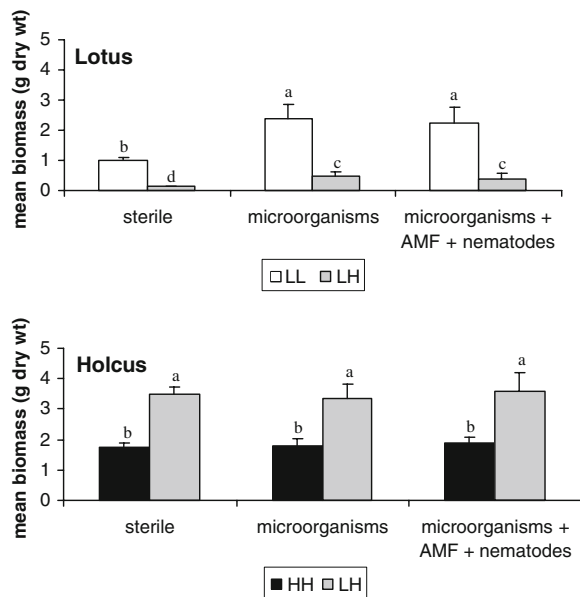
An interaction between plant combination and soil community composition ( $F_{[4,45]} = 11.36$ ,  $P < 0.001$ ) affected the total shoot biomass in the pots: *Lotus* monocultures produced the lowest shoot biomass in “sterile” soil, and tended to have the greatest biomass when soil microorganisms had been added; *Holcus* monocultures and mixtures ranged in between (Fig. 1). The total root biomass per pot was affected by plant combination ( $F_{[2,45]} = 30.59$ ,  $P < 0.001$ ) with *Lotus* monocultures having lower root biomass than *Holcus* monocultures or mixtures (Fig. 1). The mean individual shoot biomass of *Lotus* was reduced in the “sterile” soil ( $F_{[2,30]} = 40.75$ ,  $P < 0.001$ ) and by interspecific competition with *Holcus* ( $F_{[1,30]} = 332.57$ ,  $P < 0.001$ ; Fig. 2). *Holcus*, on the other side, had higher shoot biomass in the presence of *Lotus* ( $F_{[1,30]} = 263.53$ ,  $P < 0.001$ ) and was not affected by the soil community composition (Fig. 2). Nodulation of *Lotus* was low in the control soil and in the presence of *Holcus* (Interaction between plant combination and soil community composition:  $F_{[2,29]} = 8.05$ ,  $P < 0.01$ ; Fig. 3). The number of *Lotus* flowers at the harvest was reduced from on average  $11 \pm 6.6$  (SD) to  $0.2 \pm 0.9$  when the plants were in competition with *Holcus* ( $F_{[1,30]} = 44.32$ ,  $P < 0.001$ ).



**Fig. 1** Effect of soil community composition on **a** the total shoot biomass, and **b** the total root biomass of *Lotus corniculatus* monocultures (LL), *Holcus lanatus* monocultures (HH), and mixtures (LH). [Means+SD; different letters indicate a significant difference between the means at  $P < 0.05$  (Tukey's HSD test). For ANOVA results see text.]

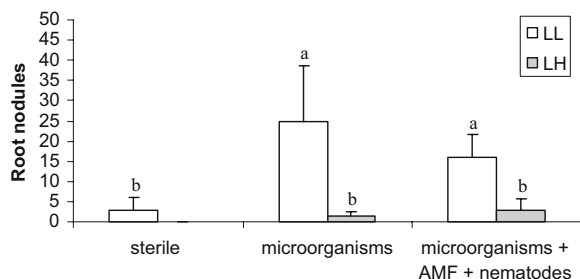
### Activated carbon

At the first harvest (week 3) shoot biomass of *Holcus* was greater than the biomass of *Lotus* ( $F_{[1,40]} = 25.07$ ,  $P < 0.001$ ; Fig. 4). *Holcus* produced a denser root system (Scheme 1) with a 2.5 fold higher biomass across treatments with and without activated carbon (*Holcus*: mean =  $0.1 \pm 0.03$  g; *Lotus*: mean =  $0.04 \pm 0.01$  g;  $F_{[1,40]} = 71.91$ ,  $P < 0.001$ ). At the second harvest (week 7) the mean shoot biomass of *Lotus* was suppressed in competition with *Holcus*, while *Holcus* tended to be promoted in presence of the legume (Interaction between plant species and plant combination:  $F_{[1,40]} = 30.00$ ,  $P < 0.001$ ). Only *Lotus* was negatively affected by activated carbon (Interaction between plant species and activated carbon:  $F_{[1,40]} = 9.95$ ,  $P < 0.01$ ; Fig. 4). The total root biomass in the pots was greatest in *Holcus* monocultures and lowest in *Lotus* monocultures (*Holcus*: mean =  $1.93 \pm$

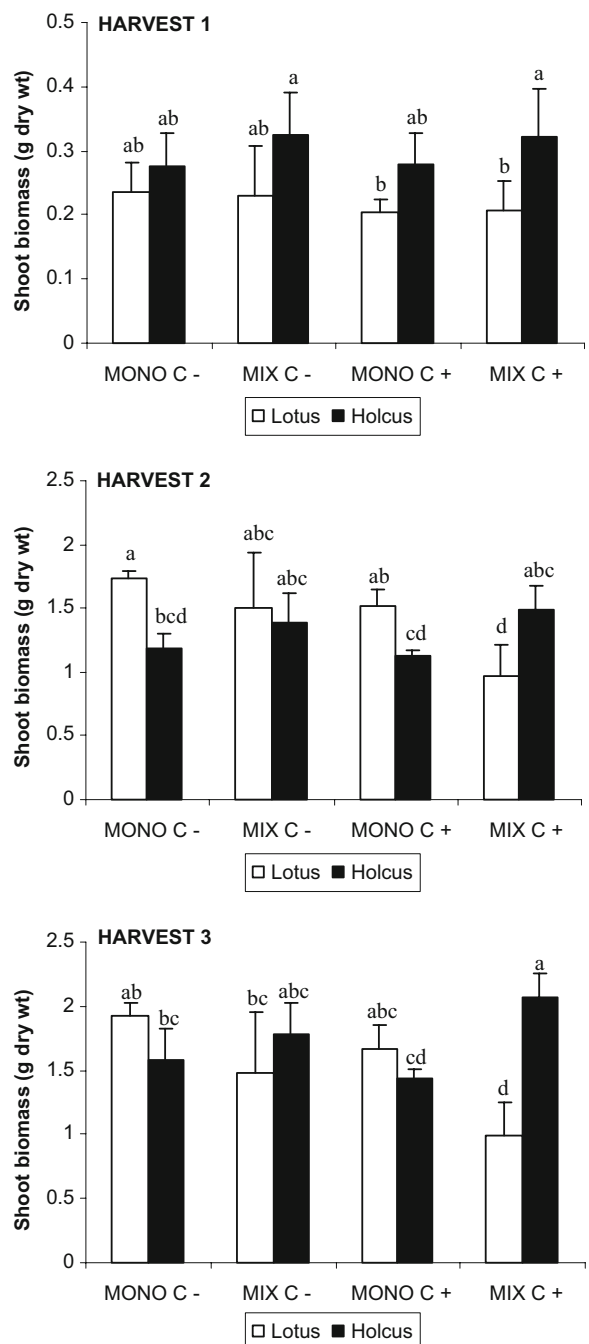


**Fig. 2** Effect of soil community composition on the mean biomass of *Lotus corniculatus* and *Holcus lanatus* individuals in *Lotus corniculatus* monocultures (LL), *Holcus lanatus* monocultures (HH), and mixtures (LH). [Means+SD; different letters indicate a significant difference between the means at  $P < 0.05$  (Tukey's HSD test). For ANOVA results see text.]

0.07 g; *Lotus*: mean=1.07±0.05 g; mixtures: mean=1.65±0.04 g;  $F_{[2,30]}=62.03$ ,  $P < 0.001$ ). At the third harvest (week 10) the same patterns were observed as in the second harvest. New was a three-way interaction between plant species, plant combination and activated carbon ( $F_{[1,40]}=5.16$ ,  $P < 0.05$ ): Only in pots with activated carbon, *Holcus* was able to strongly suppress *Lotus*, while in the monocultures *Lotus* tended to build up more biomass than *Holcus* and both plant species were slightly suppressed by activated carbon in the monocultures (Fig. 4). The



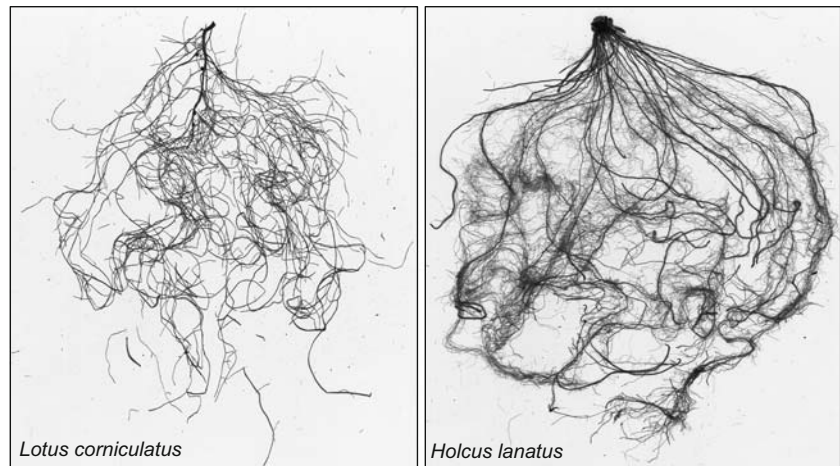
**Fig. 3** Effect of soil community composition on the number of nodules of *Lotus corniculatus* main roots in monocultures (LL), and mixtures (LH). [Means+SD; different letters indicate a significant difference between the means at  $P < 0.05$  (Tukey's HSD test). For ANOVA results see text.]



**Fig. 4** Effect of plant combination (*mono* monoculture, *mix* mixture) and activated carbon (C – without activated carbon, C + with activated carbon) on the mean biomass of *Lotus corniculatus* and *Holcus lanatus* individuals at harvest 1 to 3 [Means+SD; different letters indicate a significant difference between the means at  $P < 0.05$  (Tukey's HSD test). For ANOVA results see text.]



**Scheme 1** Root system of *Lotus corniculatus* and *Holcus lanatus* from mono-cultures in experimental soil, without activated carbon



number of *Lotus* flowers was reduced in interspecific competition with *Holcus* and by activated carbon; the magnitude of the effects changed with time (Interaction between plant combination and time:  $F_{[7,140]}=6.08$ ,  $P<0.001$ ; Interaction between activated carbon and time:  $F_{[7,140]}=2.12$ ;  $P<0.05$ ; Fig. 5). The number of nodules increased over time ( $F_{[2,40]}=36.54$ ,  $P<0.001$ ) and was reduced in competition with *Holcus* ( $F_{[1,20]}=14.05$ ,  $P<0.01$ ) and by the presence of activated carbon ( $F_{[1,20]}=5.59$ ,  $P<0.05$ ; Fig. 6).

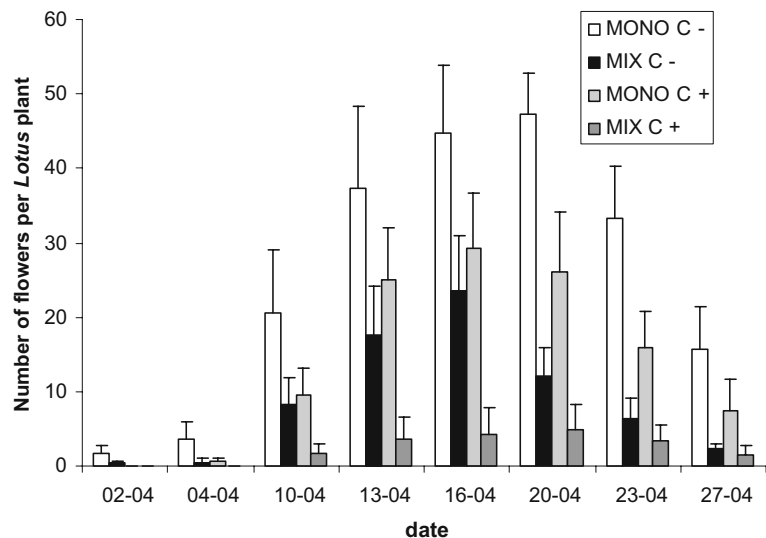
## Discussion

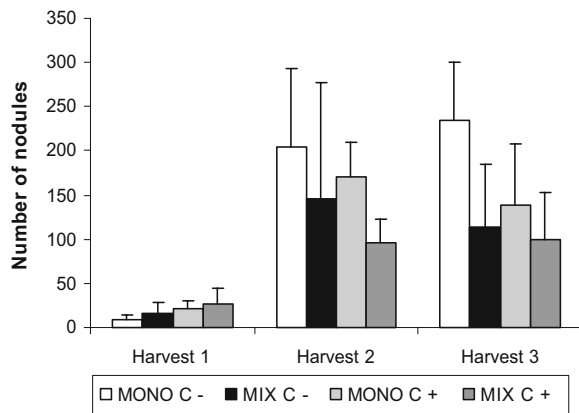
Belowground biotic interactions played a crucial role in the grass-legume competition. Mainly the presence

of soil microorganisms affected plant competition; legumes seem to rely on the symbiosis with  $N_2$ -fixing bacteria (rhizobia) to be competitive against grasses. The addition of activated carbon reduced nodulation, growth and flowering of *Lotus*, probably due to a deterred communication between the legume and rhizobia, and had negative consequences for the competitive ability of the legume.

Soil community composition affected *Lotus* and *Holcus* differentially. While the grass was not affected by the soil community composition, the legume suffered in the “sterile” control soil. Since legumes rely on  $N_2$ -fixing bacteria (rhizobia) for growth, this was not surprising. Consistently with a former study (van der Heijden et al. 2006) *Lotus* required rhizobia to successfully coexist with another plant species.

**Fig. 5** Effect of plant combination (*mono* monoculture, *mix* mixture) and activated carbon (*C* – without activated carbon, *C* + with activated carbon) on number of flowers of *Lotus corniculatus* during the course of the experiment (Means+SD. For RANOVA results see text.)





**Fig. 6** Effect of plant combination (*mono* monoculture, *mix* mixture) and activated carbon (*C* – without activated carbon, *C* + with activated carbon) on the number of nodules of *Lotus corniculatus* (Mean $\pm$ SD. For RANOVA results see text.)

Thus, monocultures of *Lotus* produced the lowest shoot biomass in the control soil, but tended to have a greater shoot biomass than *Holcus* monocultures or mixtures in the more complex soils containing a variety of soil microorganisms. The total root biomass in *Lotus* monocultures was lower than in *Holcus* monocultures and mixtures due to the extensive root growth of *Holcus*. In general, *Lotus* plants suffered from both the absence of microorganisms and the interspecific competition with *Holcus*. In a study on a tropical grass-legume mixture (Trannin et al. 2000) the establishment of a legume was suppressed by an aggressively growing grass. However, the legume established faster when inoculated with AMF, and became dominant, when the system became N limited. In the first experiment of our study, the shoot biomass, flowering, and number of nodules of *Lotus* were suppressed in the presence of *Holcus*, irrespective of the soil community composition and the likely N limitation of the soil. Thus, the presence of AMF and nematodes in the more complex soil did not change the interspecific competition. However, this might have been due to low abundances of AMF and nematodes in this soil treatment. In contrast, *Holcus* profited from the presence of *Lotus* and was not affected by the soil community composition treatments. The higher aboveground biomass of *Holcus* plants competing with *Lotus* compared to intraspecific competition might be explained by the belowground competitive superiority of *Holcus*. The fast and extensively growing roots of *Holcus* are able to outcompete *Lotus* roots, but are impeded by the roots

of conspecifics. An alternative hypothesis is that *Holcus* profits from the N<sub>2</sub> fixation by *Lotus*, since transfer of fixed N from legumes to grasses has been reported, albeit in small amounts (Ledgard et al. 1985; Giller et al. 1991). The lack of soil community composition effects on *Holcus* in contrast to *Lotus* is consistent with a recent study (Macel et al. 2007) that documents no adaptation of *Holcus* to local soil, but a transient home soil advantage for *Lotus*.

Grasses are known to exude allelochemicals (Sánchez-Moreiras et al. 2003). Allelochemicals released from plant residues can reduce the nodulation and growth of legumes (Wardle et al. 1994; Batish et al. 2007). Thus, we added activated carbon to half of the pots to adsorb root exudates and to compare the intra- and interspecific plant competition in the presence and the absence/reduction of potential allelopathic compounds (Inderjit and Callaway 2003). Contradictory to our expectations, activated carbon did not reduce the competitive ability of *Holcus* against *Lotus*, but negatively affected the nodulation, growth and flowering of the legume. The negative impact of activated carbon on *Lotus* was probably due to a negative direct effect on its symbiosis with rhizobia. Legumes attract rhizobia by exuding chemo-attractants, the first step in the establishment of the symbiosis (Cooper 2007). Only in the presence of activated carbon *Holcus* was able to suppress *Lotus* in interspecific competition. In contradiction to the first experiment, *Holcus* was not dominant (in terms of aboveground biomass) in the soil without activated carbon, in spite of its negative effects on nodulation of *Lotus*. Because we used natural soil (i.e. not sterilized) in the second experiment, the abundances of soil organisms such as rhizobia, AMF and plant-feeding nematodes were likely higher than in the reinoculated gamma-sterilized soil from the first experiment. Since AMF can stimulate nodulation and growth of legumes (Crush 1974) and *Holcus* is sensitive to plant-feeding nematodes (Verschoor et al. 2002), this might have changed the grass-legume competition in favour of the legume. However, the number of flowers of *Lotus* was strongly reduced in competition with the grass, indicating a negative effect on its fitness.

The present experiment also shows additional drawbacks of using activated carbon in studies on allelopathy to those discussed by Inderjit and Callaway (2003). Activated carbon adsorbs compounds responsible for allelopathic effects, but probably also

signalling compounds important for the interaction between plants and microorganisms. Because activated carbon inhibited the nodulation of *Lotus* in our experiment, potential allelopathic effects of *Holcus* root exudates could not be detected. However, the extensive root growth of *Holcus* suggests that the direct competition of roots for space and resources might be more important than an allelopathic inhibition of nodulation.

Generally, we observed that the symbiosis of the legume with  $N_2$ -fixing bacteria plays a crucial role in the grass-legume competition. When the symbiosis was deterred, either by a depleted soil community composition or by activated carbon, the legume was outcompeted by the grass. Probably, the fast growing and dense root system of *Holcus* directly impeded the root growth and nodulation of *Lotus*. In natural soil, however, *Holcus* was not able to suppress the shoot biomass of *Lotus*, despite its negative effects on flowering and nodulation. We propose that below-ground biotic interactions play an important role in plant competition with consequences for plant community structure.

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