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ORIGINAL PAPER

Interactions between mycorrhizal fungi and Collembola: effects on root structure of competing plant species

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Abstract Mycorrhizal fungi influence plant nutrition and therefore likely modify competition between plants. By affecting mycorrhiza formation and nutrient availability of plants, Collembola may influence competitive interactions of plant roots. We investigated the effect of Collembola (*Protaphorura fimata* Gisin), a mycorrhizal fungus (*Glomus intraradices* Schenck and Smith), and their interaction on plant growth and root structure of two plant species, *Lolium perenne* L. (perennial ryegrass) and *Trifolium repens* L. (white clover). In a laboratory experiment, two individuals of each plant species were grown either in monoculture or in competition to the respective other plant species. Overall, *L. perenne* built up more biomass than *T. repens*. The clover competed poorly with grass, whereas the *L. perenne* grew less in presence of conspecifics. In particular, presence of conspecifics in the grass and presence of grass in clover reduced shoot and root biomass, root length, number of root tips, and root volume. Collembola reduced shoot biomass in *L. perenne*, enhanced root length and number of root tips, but reduced root diameter and volume. The effects of Collembola on *T. repens* were less pronounced, but Collembola enhanced root length and number of root tips. In contrast to our hypothesis, changes in plant biomass and root structure in the presence of Collembola were not associated with a reduction in mycorrhizal formation. Presumably, Collembola affected root structure via changes in the amount of nutrients available and their spatial distribution.

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Introduction

One of the most important systems affecting plant nutrition is the symbiosis of plant roots with mycorrhizal fungi (Smith and Read 1997). Mycorrhizal fungi facilitate plant nutrient uptake, in particular that of phosphate, and also that of other nutrients, such as zinc and copper. Additionally, the symbiosis can provide the plant with inorganic nitrogen (Javelle et al. 1999; Hawkins et al. 2000; Hawkins and George 2001). The functioning of mycorrhizas, however, is affected by other biota. Mycorrhizal fungi are imbedded in a complex food web of decomposer invertebrates including soil arthropods, such as Collembola. Collembola graze on hyphae and spores of arbuscular mycorrhizal fungi (Moore et al. 1987; Bakonyi et al. 2002), and this may significantly affect plant growth (Kaiser and Lussenhop 1991; Gange 2000; Kreuzer et al. 2004).

The effect of Collembola on mycorrhizal functioning has been shown to be density dependent, with high Collembola densities hampering but low densities increasing mycorrhizal nutrient transfer to plants (Ek et al. 1994). Reduced mycorrhizal functioning might be due to lower infection of roots with mycorrhizal fungi (Lussenhop 1996) caused by feeding on spores and hyphae (Klironomos and Ursic 1998; Bakonyi et al. 2002). The increase in mycorrhizal functioning at low densities of Collembola is likely due to a stimulation of hyphal growth and functioning (Kandeler et al. 1999; Gange 2000; Cragg and Bardgett 2001). In addition, Collembola might also beneficially affect ectomycorrhizal fungi and increase root infection by transporting spores. It has been shown that spores of more than

100 fungal species adhere to the body surface of *Onychiurus subtenuis* (Visser et al. 1987).

Most Collembola species preferentially feed on saprotrophic rather than mycorrhizal fungi (Klironomos and Ursic 1998; Schreiner and Bethlenfalvay 2003). Selective grazing of Collembola on fungi may result in changes in the structure of fungal communities, e.g., by decreasing the competitive strength of saprotrophic fungi and increasing that of mycorrhizal fungi (Sabatini and Innocenti 2000; Tiunov and Scheu 2005). Changes in the structure of the soil fungal community likely result in changes in plant nutrition and therefore affect plant growth. Furthermore, Collembola affect plant growth by increasing nutrient availability by feeding on bacteria and fungi, and mobilising microbial nutrient pools (Lussenhop 1992; Theenhaus et al. 1999; Filser 2002; Cole et al. 2004). Plant roots respond to modified nutrient availability by proliferation and elongation even though shoot and root biomass may remain unaffected (Hodge et al. 1999; Endlweber and Scheu 2006).

By changing plant nutrition, root growth, and root structure, Collembola not only affect plant growth but likely also plant competition. In the laboratory, Collembola indeed increased the competitive strength of *Trifolium repens* L. against *Lolium perenne* L. (Kreuzer et al. 2004). The present experiment builds on these results by investigating if these changes are mediated by mycorrhiza. We hypothesize that changes in plant biomass and root structure are due to a reduction in mycorrhizal formation by Collembola. Therefore, we investigated the effects of Collembola on arbuscular mycorrhizal fungus infection, plant nutrient uptake, and root morphology of *L. perenne* and *T. repens* growing in monoculture and in combination of both plant species.

Materials and methods

The experiment was conducted in a temperature-controlled greenhouse (16 h light, 18°C). Rhizotrons (height 35 cm, width 15 cm, thickness 1 cm) were filled with 280 g soil taken from the upper 20 cm of a set-aside field (early successional stage) in Bad Lauchstädt near Halle (Saxony-Anhalt, Germany). The soil is a chernosem with an average pH of 7.14 and an average content of 10.19 μg PO_4^- per gram of soil. Carbonate-extractable phosphate was extracted as reported by Olsen and Sommers (1982). Average ammonium and nitrate contents were 0.43 μg NH_4^+ per gram of soil and 0.96 μg NO_3^- per gram of soil, respectively. Mineral N was extracted from subsamples and was determined as reported by Keeney and Nelson (1982).

The soil was sieved (1 cm mesh) and autoclaved at 120°C for 2 h for defaunation and elimination of mycorrhizal fungi. It was stored for 3 days at 15°C after autoclaving and then filled into the experimental containers. Fresh soil (172 g dry weight) was suspended in 200 ml distilled water to reinoculate the soil with microorganisms. The suspension (150 ml) was filtered through 25 μm gauze to exclude mycorrhizal fungus spores and made up to 750 ml with distilled water. Soil suspension (12 ml) was evenly distributed over the soil of each rhizotron.

Seven-day-old seedlings of *L. perenne* and *T. repens* were transplanted into the rhizotrons to establish the following treatments in a replacement series design: (1) two seedlings of *L. perenne*, (2) one seedling of *L. perenne* and one seedling of *T. repens*, and (3) two seedlings of *T. repens*. Each treatment was inoculated with or without mycorrhizal fungi and with and without Collembola. Each treatment was replicated five times giving a total of 60 rhizotrons. Mycorrhizal fungus (14 g) as spores and hyphae of *Glomus intraradices* Schenck and Smith (Dr. C. Grotkass, Institut für Pflanzenkultur, Schnega, Germany) was evenly spread over the soil in each rhizotron. Non-mycorrhizal treatments received the same amount of inoculum which had been autoclaved (120°C, 2 h). To control for the potential effects caused by microorganisms other than mycorrhizal fungi in the inoculum, 12 ml of a filtrate of the inoculum was added to each experimental container. The filtrate was prepared by suspending 100 g of the inoculum in 800 ml distilled water and filtered through 25 μm gauze. Half of the rhizotrons received 100 collembolans of the euedaphic species *Protaphorura fimata* Gisin. The rhizotrons were watered with 15 ml distilled water every other day throughout the experiment.

Plants were harvested after 8 weeks. Shoots were dried at 60°C for 3 days and then weighed. Dried shoots were milled in a ball mill (Retsch, Haan, Germany), and the shoot C and N contents were analyzed by an elemental analyzer (Carlo Erba, Milan, Italy). Plant roots were washed and scanned. Images were analyzed in terms of root length, number of root tips, root diameter, and root volume using WinRHIZO (Regent Instruments, Sainte-Foy, Canada). Collembola floating on the water surface during root washing were collected and counted. The roots were weighed, and a subsample was bleached by boiling in 1 N KOH. Then, the roots were dyed in 10 ml 1 N HCl mixed with two drops of ink (Quink, Parker Permanent Blue, Germany) and bleached in a mixture of 10 ml lactic acid and 10 ml distilled water. Colonization of roots by mycorrhizal fungi was analyzed using the gridline intersection method (Giovannetti and Mosse 1980). To determine root biomass, roots were dried at 60°C for 3 days and then weighed.

The experiment was set up in a complete factorial design with three factors: plant combination (con- and heterospecifics), Collembola (with and without), and mycorrhiza (with and without). The effects of these factors on above and belowground biomass, root length,

Table 1 *F*-values of a three-factor ANOVA on the effects of Collembola, presence of con-/heterospecific competitors, and mycorrhiza on shoot biomass, root biomass, root volume, root diameter, root length, and the number of root tips of *Lolium perenne* (n=5)

		Shoot biomass		Root biomass		Root volume		Root diameter		Root length		Root tips	
	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Collembola (Coll.)	1	5.72	0.0228	3.22	0.0823	131.86	<0.0001	42.18	<0.0001	104.60	<0.0001	5.72	0.0228
Plant combination (Com.)	1	22.59	<0.0001	0.05	0.8201	23.70	<0.0001	0.14	0.7117	23.93	<0.0001	22.59	<0.0001
Mycorrhiza (Myc.)	1	0.19	0.6629	0.02	0.8804	0.98	0.3298	0.12	0.7317	2.77	0.1061	0.19	0.6629
Coll. × Com.	1	2.80	0.1043	1.94	0.1728	32.36	<0.0001	9.69	0.0039	20.49	<0.0001	2.80	0.1043
Coll. × Myc.	1	0.85	0.3635	0.05	0.8201	0.44	0.5114	0.14	0.7090	0.04	0.8417	0.85	0.3635
Com. × Myc.	1	0.29	0.5945	0.21	0.6522	0.24	0.6266	0.35	0.5597	1.45	0.2379	0.29	0.5945
Coll. × Com. × Myc.	1	0.05	0.8164	0.18	0.6708	2.63	0.1146	1.95	0.1724	4.17	0.0494	0.05	0.8164

df Degrees of freedom

number of root tips, root diameter, root volume, and C and N content were analyzed by three-factor ANOVA. In treatments with conspecific competitors (monocultures), the means of the dependent variables of the two plant individuals per rhizotron were used for the analyses. Collembola density and mycorrhizal fungus inoculation were analyzed by two-factor ANOVA with mycorrhiza and plant competition as independent variables. Differences between means were inspected using Tukey's honestly significant difference test. Statistical analyses were performed using the ANOVA procedure in SAS 6.12 (SAS Institute, Cary, NC, USA).

Results

Plant combination

The shoot yield of *L. perenne* was significantly higher when grown in combination with *T. repens* compared to

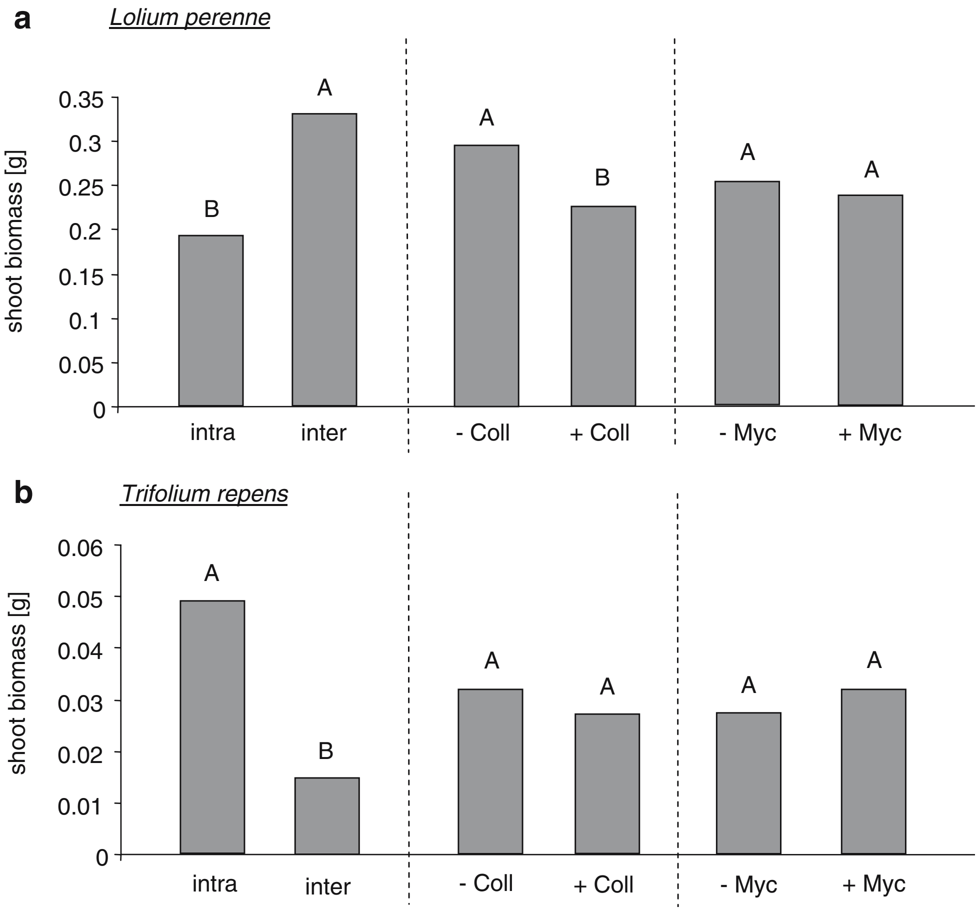

Fig. 1 Effect of presence of con- and heterospecific competitors, Collembola, and mycorrhization on shoot biomass of *Lolium perenne* and *Trifolium repens*, respectively. *Bars sharing the same letter* are not significantly different (Tukey's honestly significant difference, $P<0.05$)

when grown in monoculture (Table 1, Fig. 1a). Increased shoot biomass was not associated with changes in root biomass. However, the roots of *L. perenne* were significantly longer (Table 1, Fig. 2a) and the number of root tips was enhanced (Table 1, Fig. 3a) when grown with *T. repens* compared to monoculture. Although the root biomass and the diameter of roots (Table 1, Fig. 4) did not differ between the treatments, the root volume of *L. perenne* was significantly increased when grown with *T. repens* (Table 1).

The shoot biomass of *T. repens* grown with conspecifics was significantly higher than when grown with *L. perenne* (Table 2, Fig. 1b). When grown with *L. perenne*, the root biomass (Table 2) and the length of roots (Table 2, Fig. 2b) of *T. repens* were significantly reduced. However, root diameter (Table 2, Fig. 4), root volume, and the number of root tips remained unaffected (Table 2).

Shoot C/N ratios in *T. repens* and *L. perenne* were not significantly affected by plant combination (average: *T. repens*: 15.389, *L. perenne*: 9.831).

Effects of mycorrhiza

Inoculation with *G. intraradices* mycorrhiza affected neither below- nor aboveground biomass of *L. perenne* (Table 1, Fig. 1a). Furthermore, inoculation of plant roots with mycorrhizal fungi did not affect root length, root volume, and root diameter nor the number of root tips (Figs. 2a, 3a and 4a).

As in *L. perenne*, the inoculation with the mycorrhizal fungus did not affect shoot or root biomass of *T. repens*, but it significantly reduced root length (Tables 1 and 2, Fig. 2b), root diameter, and the number of root tips (Table 2, Figs. 3b and 4b). Furthermore, the extent of mycorrhizal inoculation of roots of *T. repens* grown with *L. perenne* significantly exceeded when grown with conspecifics ($F_{5,24}=4.74$, $P=0.0410$).

The average colonization of roots of *L. perenne* by *G. intraradices* (86.66% of root length) generally exceeded that of *T. repens* (67.97%). The inoculation with mycorrhizal fungi affected neither the C/N ratio of *T. repens* nor that of *L. perenne* (average: *T. repens*: 15.336, *L. perenne*: 9.809).

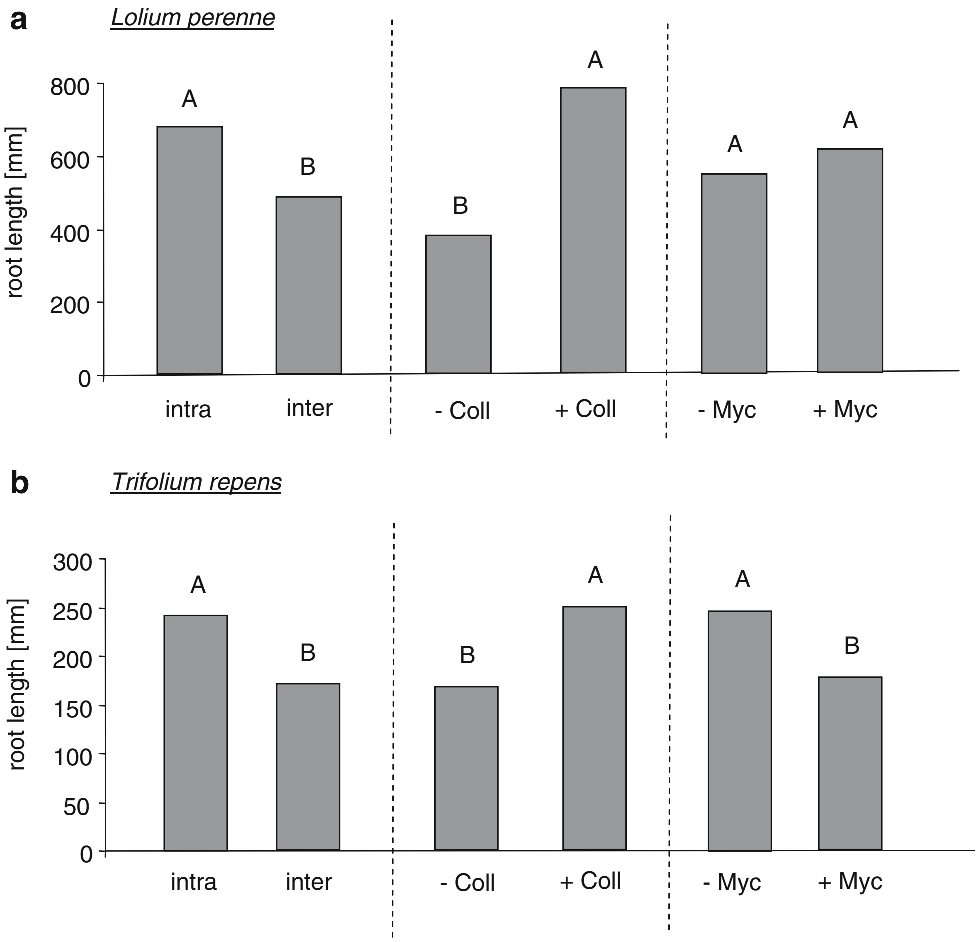

Fig. 2 Effect of presence of con- and heterospecific competitors, Collembola, and mycorrhization on root length of *Lolium perenne* and *Trifolium repens*, respectively. *Bars sharing the same letter* are not significantly different (Tukey's honestly significant difference, $P<0.05$)

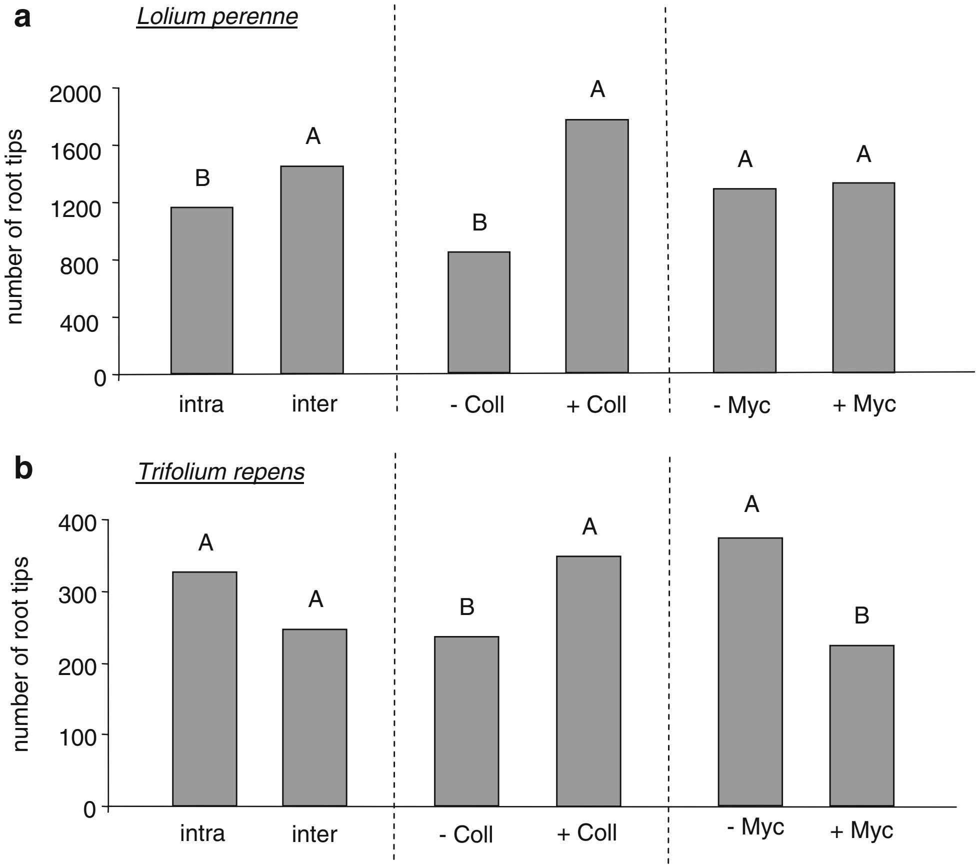

Fig. 3 Effect of presence of con- and heterospecific competitors, Collembola, and mycorrhization on root diameter of *Lolium perenne* and *Trifolium repens*, respectively. *Bars sharing the same letter* are not significantly different (Tukey's honestly significant difference, $P<0.05$)

Effects of Collembola

Collembola significantly reduced shoot but not root biomass of *L. perenne* (Table 1, Fig. 1a). However, Collembola significantly increased root length (Table 1, Fig. 2a) and the number of root tips (Table 1, Fig. 3a) but decreased root volume and root diameter (Table 1, Fig. 4a).

Collembola did not affect above- and belowground biomass, root volume, and root diameter of *T. repens*. However, they enhanced the length of roots of *T. repens* but reduced the number of root tips (Table 2, Figs. 1a, 2a, 3a, and 4a). In contrast, Collembola significantly reduced the colonization of roots of *T. repens* by mycorrhizal fungi by about 20% ($F_{3,26}=5.23$, $P=0.0327$) but did not affect mycorrhizal infection of roots of *L. perenne*. Collembola generally did not affect the C/N ratio of the two plant species (average: *T. repens*: 15.338, *L. perenne*: 9.809).

Inoculation of plant roots with *G. intraradices* generally did not affect Collembola density, but the number of Collembola significantly differed between the competition treatments ($F_{5,24}=13.79$, P=0.0006), with an average of 162 individuals per rhizotron in *T. repens* monocultures and an approximately three times higher density in *L. perenne* monocultures and in combinations of *T. repens* and *L. perenne* (average of 403 and 435 individuals per rhizotron, respectively).

Discussion

Competition is one of the most important factors structuring plant communities. Plant responses may differ between intra- and interspecific competition depending on plant species and plant functional group (Gersani et al. 2001; Maina et al. 2002). Plant competitiveness varies with plant root structure and root foraging strategy (Lodge 2000; Rajaniemi and Reynolds 2004). Hence, plant competitiveness likely increases with the growth rate of roots and the extension of the root system (Aerts 1999). In the present experiment, *L. perenne* grew faster and built up significantly more biomass than *T. repens*. The presence of *L. perenne* was associated with a reduced biomass of *T. repens* compared to monoculture treatments. This is consistent with the findings of other studies demonstrating a competitive superiority of ryegrass over clover (Munoz and Weaver 1999; Lucero et al. 1999). Strong competitiveness of *L. perenne* likely is due to the ramified root system which is characteristic for grasses and allows effective uptake of nutrients (Stone et al. 1998). Furthermore, in soils with high N availability, the competitive advantage of nitrogen-fixing legumes is abrogated. Autoclaving soil, as done in the present experiment to eliminate mycorrhiza, mobilizes nutrients, especially N, and may have contributed

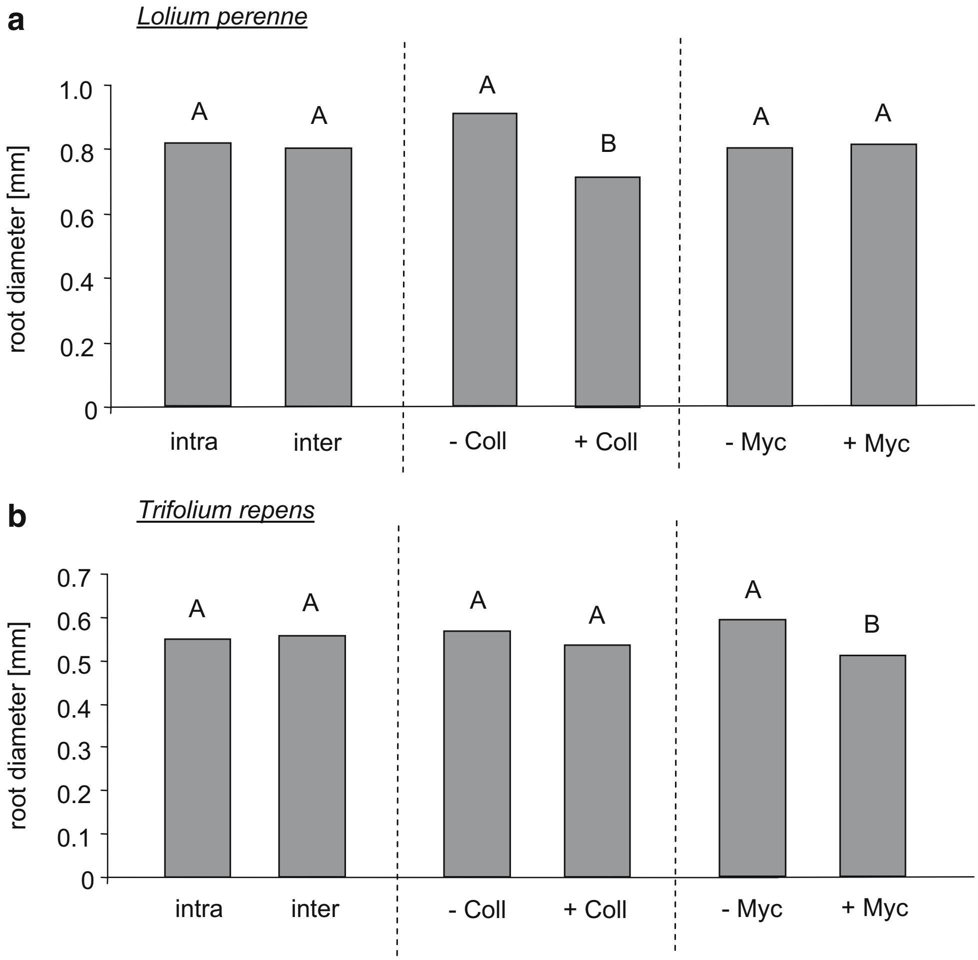

Fig. 4 Effect of presence of con- and heterospecific competitors, Collembola, and mycorrhization on root number of root tips of *Lolium perenne* and *Trifolium repens*, respectively. *Bars sharing the same letter* are not significantly different (Tukey's honestly significant difference, $P<0.05$)

to the low competitiveness of *T. repens* in our experiment. This is supported by the low number of nodules observed for *T. repens*.

The different responses of the two plant species to monoculture and the combined treatment are probably due to the different growth rates of both plant species. The grass had a higher growth rate than the clover. Therefore, competition between conspecifics of *L. perenne* was higher in the limited space of the rhizotrons compared to monocultures of *T. repens*. Furthermore, the grass outcompeted clover in the combined treatments.

In addition to shoot biomass, presence of con- and heterospecific competitors also affected root structure; similar results have been documented (Gersani et al. 1998). Intra- and interspecific competition often results in an increase in root biomass (Maina et al. 2002; O'Brien et

Table 2 *F*-values of a three-factor ANOVA on the effects of Collembola, presence of con-/heterospecific competitors, and mycorrhiza on shoot biomass, root biomass, root volume, root diameter, root length, and the number of root tips of *Trifolium repens* ($n=5$)

		Shoot biomass		Root biomass		Root volume		Root diameter		Root length		Root tips	
	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Collembola (Coll.)	1	0.55	0.4625	0.31	0.5795	2.31	0.1396	0.79	0.3801	6.98	0.0131	4.39	0.0450
Plant combination (Com.)	1	24.93	<0.0001	4.85	0.0347	0.47	0.4966	0.08	0.7755	4.96	0.0338	2.01	0.1672
Mycorrhiza (Myc.)	1	0.51	0.4784	1.31	0.2601	3.45	0.0733	5.30	0.0287	5.45	0.0267	7.13	0.0123
Coll. × Com.	1	1.45	0.2381	0.06	0.8051	1.88	0.1809	0.73	0.3990	3.28	0.0806	0.41	0.5249
Coll. × Myc.	1	1.05	0.3131	0.00	1.0000	0.70	0.4099	1.30	0.2644	0.30	0.5905	0.01	0.9124
Com. × Myc.	1	2.07	0.1599	1.15	0.2919	0.40	0.5306	0.06	0.8112	0.15	0.6975	0.73	0.3985
Coll. × Com. × Myc.	1	0.10	0.7527	1.14	0.2925	4.45	0.0436	2.29	0.1412	8.78	0.0060	6.61	0.0155

df Degrees of freedom

al. 2005). Generally, competition between plant roots is more intense among plants with similar root morphology (Rubio et al. 2001). In the present experiment, *L. perenne* produced longer roots, more root tips, and an enhanced root volume when competed with *T. repens* as compared to when grown with conspecifics. In contrast, *T. repens* produced longer roots when grown in monoculture as compared to when grown in competition with *L. perenne*. Root proliferation is strongly affected by the availability of nutrients and allows plants to exploit resources to the disadvantage of the competitor (Hodge et al. 1999; Gersani et al. 2001). There is evidence that plant species are able to differentiate conspecific and heterospecific roots and adjust the response of the root system accordingly (Huber-Sannwald et al. 1996).

Mycorrhiza

The response of plants to inoculation with AM fungi species varies with the mycorrhizal fungus (Joner and Leyval 2001; Rogers et al. 2001; Klironomos 2003). In the present experiment, root colonization with mycorrhizal fungi in *L. perenne* exceeded that in *T. repens*. Nevertheless, plant growth and root morphology in *L. perenne* were little affected by mycorrhiza, whereas in *T. repens*, mycorrhiza reduced root length, the number of root tips, and root diameter.

Mycorrhizal fungi allow plants to reduce investment into roots because mycorrhizal hyphae compensate for reduced extension of the root system (Smith and Read 1997; Harrison 1997; van der Heijden 2004). Colonization of roots by mycorrhizal fungi therefore likely affects competition of plant species (van der Heijden et al. 2003; Smith et al. 1999). Indeed, in previous experiments, mycorrhizal fungi increased the competitive strength of clover against ryegrass (Hamel et al. 1992; Joner and Leyval 2001). This might have been due to higher colonization of roots by mycorrhizal fungi of the legume compared to the grass. However, in the present experiment, mycorrhizal fungi did not increase the competitiveness of clover. This might have been due to the higher colonization by mycorrhizal fungi of the *L. perenne* roots compared to the roots of *T. repens*. Colonization by mycorrhizal fungi is probably correlated with the plant nutrient status. Blanke et al. (2005) demonstrated a negative correlation between root colonization of *Artemisia vulgaris* by AMF and tissue N concentration. Therefore, the differences in colonization by mycorrhizal fungi are possibly due to the different nutrient contents.

Collembola

Collembola may stimulate or reduce plant nutrition and growth (Harris and Boerner 1990; Bardgett and Chan 1999; Scheu et al. 1999; Lussenhop and Bassirirad 2005). In addition, Collembola may significantly affect root growth without affecting shoot growth (Scheu et al. 1999; Endlweber and Scheu 2006). In the present experiment, Collembola increased root length and the number of root tips in both plant species but reduced shoot biomass, root volume, and root diameter in *L. perenne*. The reduction in shoot biomass of *L. perenne* was more pronounced when grown with *T. repens*, suggesting that Collembola reduced the competitive superiority of *L. perenne* over *T. repens*. These findings and previous experiments (Kreuzer et al. 2004; Partsch et al. 2006) suggest that Collembola generally increase the competitive strength of legumes against grasses. The increase in the competitive strength of legumes may be caused by increased nodule occupancy in legumes in the presence of Collembola (Lussenhop 1993).

Increased root elongation and number of root tips likely reflect an increase in the availability of nitrate (Zhang and Forde 2000; Mantelin and Touraine 2004). Collembola may increase N availability in the rhizosphere via enhancing microbial N mineralization and by forming nutrient-rich patches through excretion (Bardgett and Chan 1999; Petersen 2000; Sjursen and Holmstrup 2004). Presumably, in the present experiment, mineral N made available by Collembola at microsites in soil, such as droppings of excreta, was nitrified quickly, and this stimulated root elongation and branching. However, the potentially increased availability of N by Collembola was not reflected by shoot N concentration. In fact, the reduction of shoot biomass by Collembola contradicts the assumption that Collembola enhanced nutrient availability to plants. This reduction might have been due to a decline in nutrients provided by mycorrhizas. Collembola have been shown to alter mycorrhization of plant roots with the effect being density dependent (Ek et al. 1994; Lussenhop 1996; Bakonyi et al. 2002). In the present experiment, Collembola reduced the colonization of roots by mycorrhiza of *T. repens*, which likely was caused by grazing on mycorrhizal hyphae. Surprisingly, however, Collembola did not significantly affect root colonization by mycorrhiza in *L. perenne* although mycorrhizal colonization of roots in *L. perenne* exceeded that in *T. repens*.

Collembola density was significantly higher in treatments with ryegrass, suggesting that they benefited from high root biomass and associated high root exudates and increased biomass of saprophytic fungi (cf. Salamon et al. 2004; Sung et al. 2006). Milcu et al. (2006) found Collembola density to be reduced in the presence of legumes, whereas it was increased in the presence of grasses.

Conclusions

The presence of Collembola alters root structure with longer and thinner roots and therefore likely affects plant resource exploitation. Although plant C and N content remained unaffected, the presence of Collembola declined shoot biomass. Overall, the results of the present experiment and previous studies suggest that the effect of Collembola depends on plant species, with grasses being more vulnerable than legumes. Therefore, Collembola likely reduce the competitive superiority of grasses over legumes. The Collembola-mediated reduction in shoot biomass and the changes in root structure were not related to the changes in mycorrhizal fungus colonization of roots. Hence, the effect of Collembola on root morphology and shoot biomass presumably is not caused by affecting plant–mycorrhiza interrelationships but possibly by direct grazing on roots and on saprotrophic fungi.

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