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Interactions between a mycophagous Collembola, dry yeast and the external mycelium of an arbuscular mycorrhizal fungus

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Abstract A plant growth system with root-free hyphal compartments was used to examine the interactions between a mycophagous Collembola (*Folsomia candida* Willem), dry yeast and an arbuscular mycorrhizal (AM) fungus [*Glomus caledonium* (Nicol. & Gerd.) Trappe and Gerdemann] in terms of Collembola reproduction, AM-hyphal length and AM-hyphal P transport. Collembola reproduction was unaffected by AM mycelium, but a supplement of dry yeast increased the Collembola population size. The addition of dry yeast increased AM-hyphal P transport by increasing hyphal length. Collembola without yeast affected neither AM-hyphal growth nor AM-hyphal P transport, whereas Collembola with yeast decreased AM-hyphal P transport by 75% after 8 weeks. The hyphal density of *G. caledonium* remained unaffected by Collembola except after 4 weeks in combination with yeast, when a 33% reduction was observed. The results of this experiment show that the interaction between *F. candida* and the external mycelium of *G. caledonium* is limited under the conditions imposed.

Key words Arbuscular mycorrhiza · Collembola · Hyphal length · Hyphal P transport

Introduction

The external mycelium of arbuscular mycorrhizal (AM) fungi constitutes an important part of the fungal mycelium in soils covered by herbaceous plants and may serve as a potential food source for mycophagous soil animals. Such an interaction between the external mycelium of AM fungi and mycophagous soil animals may have detrimental consequences for AM symbiosis (Fitter and Garbaye 1994).

Many Collembola are known to be mycophagous (Bödvarsson 1970; Petersen and Luxton 1982) and four Collembola species were found to graze on spores and hyphae from germinating spores of two AM fungi (Moore et al. 1985). Furthermore, four out of five Collembola species tested preferred to graze on AM rather than non-AM roots (Thimm and Larink 1995). Manipulation of Collembola numbers in experiments with AM and non-AM plants also led to the suggestion that Collembola graze on the external mycelium (Warnock et al. 1982; Finlay 1985; Harris and Boerner 1992). However, this was not confirmed in other experiments (Kaiser and Lussenhop 1991; Klironomos and Kendrick 1995).

The objective of this present work was to further examine the interactions between external mycelium of AM fungi and Collembola, in terms of Collembola reproduction, hyphal length and hyphal P transport. As Collembola are known to reproduce on yeast, this was included as an additional growth substrate.

Materials and methods

Experimental design

Plants with or without AM fungi were grown in compartmented growth units made from PVC tubes (4.5 cm internal diameter) which consisted of a central root compartment (32.5 cm) separated from two lateral root-free hyphal compartments (7 cm) by means of a 37-μm nylon mesh (Fig. 1). Collembola were either present or absent from the soil in both hyphal compartments for each plant. The four main treatments (–/+ AM × –/+ Collembola) had 12 replicates with a total of 48 plants. Yeast was supplied to one hyphal compartment for each plant giving a total of eight treatments. Four replicate plants of each main treatment were harvested after 4, 6 and 8 weeks.

Soil, mycorrhizal fungus and Collembola

The soil was a 1:1 (w/w) mixture of a sandy loam and quartz sand, which had been partially sterilized by irradiation (10 kGy,

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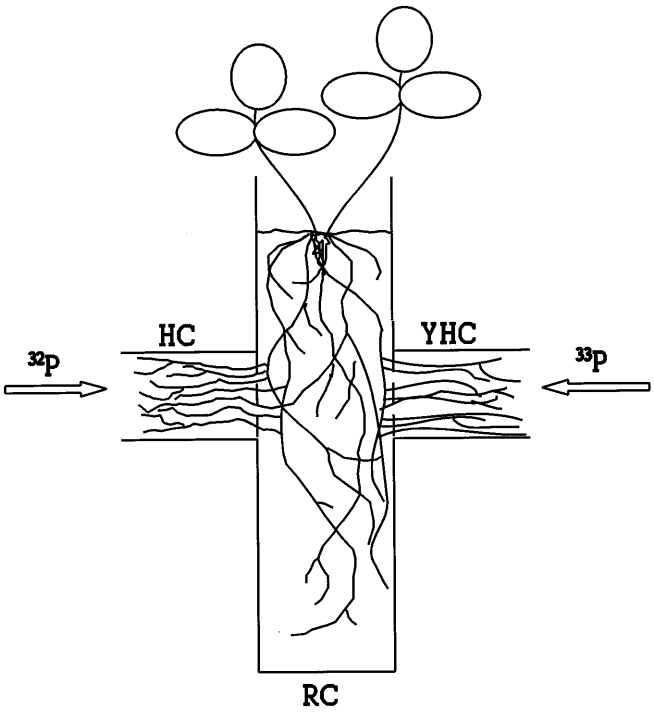

Fig. 1 Design of the three-compartment growth system with a central root compartment (*RC*), a hyphal compartment without yeast (*HC*) and a yeast-hyphal compartment with yeast (*YHC*). The application of tracer isotopes is indicated by *arrows*

10 MeV electron beam). The soil mixture had a pH of 6.1 and contained 8 mg kg^{-1} soil of 0.5 M $NaHCO_3$–extractable P. The following nutrients were mixed into the soil (mg kg^{-1} soil): K_2SO_4 (70), $CaCl_2$ (70), $CuSO_4 \cdot 5H_2O$ (2.2), $ZnSO_4 \cdot 7H_2O$ (5), $MnSO_4 \cdot 7H_2O$ (10), $CoSO_4 \cdot 7H_2O$ (0.33), $NaMoO_4 \cdot 2H_2O$ (0.2) and $MgSO_4 \cdot 7H_2O$ (20). Soil for non-AM treatments received 25 mg P kg^{-1} as KH_2PO_4 in order to obtain similar growth rates in AM and non-AM plants. The central root compartments were filled with 700 g soil. The upper 400 g of AM treatments was a mixture of 325 g soil and 75 g crude inoculum of *Glomus caledonium* (Nicol. & Gerd.) Trappe and Gerdeman isolate RIS42 (BEG15). Each root-free compartment received 75 g soil, and 25 mg dry yeast was mixed with the soil in the yeast-hyphal compartment (YHC) but not in the hyphal compartment (HC). The 75 g soil in both HC and YHC was applied in two lots of 50 g and 25 g for half of the plants (+Collembola treatments). Twenty adult individuals (about 1 mm) of *Folsomia candida* Willem were placed on top of the 50 g soil and covered by the remaining 25 g soil. This initial Collembola density corresponds to approximately 350 individuals dm^{-3}. The Collembola had been kept in a soil/sand mixture at room temperature and fed on dry yeast. A plastic vial was pushed into the root-free compartments to hold the soil in place. In order to reintroduce microorganisms other than AM fungi, all growth units recieved 10 ml of a soil filtrate obtained from a suspension of 100 g inoculum in 1 l H_2O, which had been sieved through a 20-μm nylon mesh. All growth units were watered to 60% of field capacity and incubated for 1 week at room temperature.

Plants and growth conditions

Two pregerminated seeds of subterranean clover (*Trifolium subterraneum* L., *cv.* Mount Barker) were sown in each growth unit and thinned to one after seedling emergence. Plants were maintained in a growth chamber with a 16/8h light/dark cycle at 21/16 °C, and Osram daylight lamps (HQ1-T 250 W/D) provided a photosynthetically active radiation of 500–550 mmol $m^{-2}s^{-1}$. The plants were relocated and watered daily by weight to maintain 60% of field capacity. Nitrogen was supplied weekly as a NH_4NO_3 solution with a total of 155 mg N per plant during the growth period.

Application of isotopes

Four days before each harvest, 167 kBq of $H_3{}^{32}PO_4$ and 167 kBq of $H_3{}^{33}PO_4$ were applied to the HC and the YHC, respectively. The isotopes were applied in a solution (2 ml) on top of the soil after removal of the plastic vial holding the soil.

Harvest and analyses

Plants were harvested after 4, 6 and 8 weeks; each harvest comprised 16 plants. The two root-free compartments were removed from each growth unit and kept at 4 °C until further analysis. Roots were washed out of the soil and a weighed subsample from between the two lateral compartments was cleared and stained for measurement of mycorrhiza formation (Kormanick and McGraw 1982) and root length by means of the line-intercept method (Newman 1966). All other plant materials were dried, weighed and analysed for ^{32}P and ^{33}P after digestion in a solution of nitric/perchloric acid (4:1 v/v). Aliquots of the diluted digest (3 ml) were mixed with 10 ml scintillation fluid. The radiotracers were counted in a Packard TR1900 liquid scintillation counter by Dual Spectrum Analysis. The soil in each root-free compartment was divided into two lots corresponding to 0–2 cm or 2–3 cm distance from the nylon mesh. The soil in the 2–3 cm labelling zone was mixed and subsamples (2×2.5 g) were dried at 40 °C and used for determination of hyphal length in the labelled area by the method of Jakobsen et al. (1992) using the grid-line intercept method (Tennant 1975). The hyphal length density of *G. caledonium* in the HC and the YHC 2–3 cm isotope labelling zone in the AM treatments was obtained by subtracting the background values obtained from the corresponding non-AM treatments. A flotation-sieving method was used to extract Collembola from all soil in the HC and in the YHC, except for the subsamples used to measure hyphal length. The soil was washed five times in water and sieved (63 μm). The Collembola were transferred with 70% ethanol from the sieve to a petri dish with glycerol and counted.

Statistics

Levels of significance of the results form the main treatments and their interaction were obtained by analysis of variance and the means were compared by $LSD_{0.05}$. Data for Collembola numbers were ln-transformed in order to obtain variance homogeneity. Statgraphics plus for Windows was used to perform the statistical tests.

Results

Plant growth and mycorrhiza formation

Plant dry weights and root length densities of both AM and non-AM plants and the colonization of AM plants were unaffected by the presence of Collembola in the root-free compartments (Table 1). The average plant dry weight of non-AM plants with and without Collembola was similar to the average plant dry weight of AM plants with and without Collembola, except after 8

Table 1 Effect of the presence of Collembola on plant dry weight, root length density and percentage of the root system colonized of *Trifolium subterraneum* plants inoculated (AM) or not (non-AM) with *Glomus caledonium*

Treatment		Plant dry weight (g)			Root length density (cm g^{-1} soil)			Percentage of root system colonized		
	Week:	4	6	8	4	6	8	4	6	8
Mycorrhiza	Collembola									
Non-AM + P	−	0.9	3.6	6.2	7.8	33.7	35.1	−	−	−
Non-AM + P	+	0.8	3.8	5.6	6.9	37.9	29.1	−	−	−
AM	−	1.0	3.4	4.5	5.5	25.8	21.5	72	56	62
AM	+	1.0	3.3	4.2	5.0	21.7	19.8	69	57	62
$LSD_{0.05}$		ns	ns	0.9	ns	8.4	7.5			
P values for ANOVA										
Mycorrhiza (M)		0.21	0.06	< 0.001	0.07	0.001	< 0.001	−	−	−
Collembola (C)		0.14	0.54	0.43	0.56	0.97	0.14	−	−	−
M × C		0.63	0.61	0.27	0.87	0.16	0.41	−	−	−

weeks, when the dry weight of AM plants was 25% less than that of non-AM plants (Table 1). The average root length densities of AM plants with and without Collembola were 34% and 36% lower than the average root length density of non-AM plants with and without Collembola after 6 and 8 weeks, respectively (Table 1). While uninoculated plants remained non-mycorrhizal, plants inoculated with *G. caledonium* had 69–72% of their root length colonized after 4 weeks. The percentage of the root length colonized decreased to 57% 2 weeks later, when total root length had increased 3.5- to 4-fold. Root length and colonization did not increase further from week 6 to week 8.

AM-hyphal length and P transport to plants

Hyphal densities in the root-free compartments of non-AM treatments were 1.02 and 1.21 m g^{-1} soil without and with yeast, respectively. These background values were unaffected by the presence of Collembola (data not presented). Yeast increased the hyphal densities of *G. caledonium*, which were 2.6-, 2.0- and 1.6-fold higher in the YHC than in the HC after 4, 6 and 8 weeks, respectively. Presence of Collembola did not affect the AM hyphal density, except after 4 weeks in combination with yeast, when the hyphal density was reduced by 33% (Table 2). The total biomass of AM hyphae in the HC of AM treatments without yeast was estimated to be 2 mg dry weight by means of a biovolume conversion factor for soil fungi (Bakken and Olsen 1983).

The uptake of ^{32}P and ^{33}P from the root-free hyphal compartments of non-AM plants was in the range 0–0.31 kBq and the measured radiotracer levels in each AM treatment were corrected by the background measured in the corresponding non-AM treatment. Total AM hyphal P uptake and transport to plants from the HC without Collembola decreased with time, but was in general higher in the presence than in the absence of dry yeast (Table 3). However, the length-specific uptake after 4 weeks was 54% and 44% lower with than without yeast, respectively, in combinations without or with Collembola (Table 3).

Table 2 Hyphal length density of *G. caledonium* in the hyphal (HC) and the yeast-hyphal (YHC) compartments with or without Collembola

Treatment		Hyphal length density (m g^{-1} soil)		
	Week:	4	6	8
Collembola	Yeast			
−	−	3.7	6.2	6.7
+	−	3.8	4.9	6.0
−	+	9.5	12.5	10.9
+	+	6.4	12.2	11.5
$LSD_{0.05}$		2.1	2.5	2.2
P values for ANOVA				
Collembola (C)		0.04	0.34	0.99
Yeast (Y)		< 0.001	< 0.001	< 0.001
Y × C		0.04	0.60	0.42

Furthermore, after 4 weeks the total hyphal uptake in treatments with Collembola tended to be smaller than in the treatments without Collembola, and after 8 weeks the total hyphal P uptake and length specific P uptake in the Collembola + yeast treatment was 75% and 76% smaller, respectively, than in the yeast-only treatment.

Collembola reproduction

Numbers of Collembola recorded in soil without yeast (HC) were either lower than or similar to the 20 individuals initially introduced, irrespective of the presence of external hyphae (Table 4). In contrast, the presence of yeast increased the population of *F. candida*, which was significantly higher than the populations recorded in non-yeast soil at 6 and 8 weeks (Table 4).

Table 3 Effect of yeast and Collembola on total AM hyphal uptake and AM hyphal length specific uptake of labelled P into plants

Treatments		Total hyphal uptake (hBq)			Length specific uptake (Bq m^{-1} hyphae)		
	Week:	4	6	8	4	6	8
Collembola	Yeast						
−	−	12.2	3.9	0.8	139.7	24.6	5.6
+	−	9.5	6.5	1.1	116.3	63.2	8.0
−	+	13.9	9.8	3.6	63.9	33.9	14.6
+	+	9.5	8.4	0.9	65.4	30.0	3.5
$LSD_{0.05}$		ns	ns	1.6	76.0	ns	7.4
P values for ANOVA							
Collembola (C)		0.13	0.82	0.03	0.67	0.19	0.09
Yeast (Y)		0.69	0.16	0.03	0.02	0.37	0.37
C × Y		0.73	0.46	0.01	0.63	0.11	0.02

Table 4 Total numbers of Collembola in root-free compartments as affected by yeast and external hyphae of *G. caledonium*. Data are ln-transformed; non-transformed figures are given in parentheses

Treatments		Total Collembola numbers		
	Week:	4	6	8
Mycorrhiza	Yeast			
−	−	1.97 (7.2)	0.96 (2.6)	1.49 (4.4)
−	+	3.12 (22.6)	4.34 (76.7)	3.41 (30.3)
+	−	2.66 (14.3)	1.21 (3.4)	2.99 (19.9)
+	+	2.74 (15.5)	3.50 (33.1)	3.94 (51.4)
$LSD_{0.05}$		1.47	1.09	1.75
P values for ANOVA				
Mycorrhiza (M)		0.77	0.43	0.11
Yeast (Y)		0.25	< 0.001	0.03
M × Y		0.32	0.16	0.43

Discussion

This is the first examination of interactions between AM fungi and Collembola without the interfering effects of roots. The study was facilitated by an experimental system where external hyphae of *G.caledonium* grew into root-free compartments in the presence or absence of *F. candida*. The densities of *F. candida* were similar to the average Collembola density in agricultural soils ($20–50 \times 10^3$ m^{-2}: Andrén and Lagerlöf 1983; Christensen et al. 1987; Lagerlöf and Andrén 1991; Krogh 1994), and were in the same range as those used in other experiments concerning effects of *F. candida* on the AM symbiosis (Warnock et al. 1982; Finlay 1985; Kaiser and Lussenhop 1991; Harris and Boerner 1992). Except for that of Kaiser and Lussenhop (1991), previous studies suggest that Collembola is a potential grazer of AM hyphae. This is further supported by field experiments in which the use of insecticides coincided with a reduced Collembola density and an increased plant dry weight and plant P content (Finlay 1985; McGonigle and Fitter 1987). In our experiment, Collembola densities in the range 210–350 individuals dm^{-3} had no impact on growth and P transport of the AM fungus when the soil received no yeast amendment. This is consistent with the results of Kaiser and Lussenhop (1991) and with recent observations that the AM-hyphal length in soil with AM roots is unaffected by a combination of six different microarthropods including four Collembola species (Klironomos and Kendrick 1995). Furthermore, the effectiveness of three AM fungi in symbiosis with *T. subterraneum* was also unaffected by *F. candida* feeding in the rooting compartment (J. Larsen, unpublished work). This inconsistency in reports on Collembola–AM fungi interactions may be related to the use of different Collembola densities and the use of different AM fungi and Collembola species.

Our conclusion that *F. candida* did not graze on AM fungi was consistent with the findings that the AM mycelium had no obvious effect on the population size of *F. candida*. The AM-hyphal biomass (2 mg dry wt) in the HC of AM treatments without yeast was too small apparently to support reproduction by the Collembola, as at least 60 mg dry yeast mixed with 30 g soil was needed to obtain a significant reproductive output from 10 individuals of *F. candida* (Krogh 1994). Populations of *F. candida* did not increase when fed *in vitro* on a surplus of AM hyphae sampled from a pot culture of *Glomus intraradices* (J. Larsen, unpublished work).

This suggests that some AM fungi may be of little nutritive value to Collembola.

In contrast to the limited interactions measured between *G. caledonium* and *F. candida*, the addition of yeast had multiple effects on both *G. caledonium* and *F. candida*. Yeast increased AM-hyphal growth and to some extent also AM-hyphal P uptake. Three mechanisms could have contributed to this stimulatory effect. Firstly, the yeast amendment possibly increased the soil microbial activity and might well have altered the composition of the microflora community. Such changes in bacteria populations have been found to modify AM function (Azcón-Aguilar and Barea 1992), and a soil leachate was found to increase the development of AM-external mycelium in sand-dune soil, probably due to the presence of AM-stimulatory bacteria in the soil leachate (Sutton and Sheppard 1975). Secondly, an increase in the level of inorganic nutrients after decomposition of added yeast may have increased AM hyphal growth. Indeed, increased levels of NH_4^+ has been found to increase AM-hyphal growth (Johansen et al. 1994), although hyphal growth seems to depend rather little on the soil P level (Li et al. 1991). Thirdly, the increased biological activity in YHC could have increased the CO_2 production in the YHC. Hyphae of AM fungi have a growth optimum at 1–2% CO_2 (Poulin et al. 1993). Accordingly, the increased hyphal growth in YHC could be related to elevated CO_2 concentrations. This possibility, however, is valid only if a marked CO_2 gradient exits between the RC and the YHC, such that the concentration in the RC is markedly higher than in the HC without yeast.

The lower AM-hyphal length in yeast-amended soil after 4 weeks in the presence than in the absence of Collembola could be explained by grazing, but it is unclear why a similar Collembola density in the treatments without yeast did not likewise reduce hyphal length. High Collembola numbers at the 8-week harvest did not affect the AM-hyphal length, but reduced the AM-hyphal P uptake and transport to plants. This less efficient length-specific AM-hyphal uptake could be due to Collembola grazing on either fine absorbing hyphae or the coarse hyphae connecting the internal and external mycelium, or both. It has been observed, that microarthropods prefer thin AM hyphae of higher branching order to coarse connecting hyphae (Klironomos and Kendrick 1996). Yeast effects on the microflora could contribute to reductions in hyphal length so that a combination of yeast and Collembola could have favoured the microflora community and, thereby, caused microbial immobilization of nutrients, including the labelled P.

In vitro feeding studies have demonstrated that mycophagous Collembola prefer specific saprophytic fungi (Klironomos et al. 1992), AM roots rather than non-AM roots (Thimm and Larink 1994) and saprophytic fungi more than AM fungi (Klironomos and Kendrick 1996). In the present study, yeast was included in order to examine in situ preferential feeding by *F. candida.* However, no safe conclusions on the feeding behavior of *F. candida* can be drawn because interactions between *F. candida* and the external mycelium of *G. caledonium* were limited and because the presence of yeast alone increased the hyphal length of *G. caledonium*.

The decline in growth of AM plants between 6 and 8 weeks coincided with a decline in AM-fungal activity. A similar decline in AM-fungal P transport was also observed by Jakobsen et al. (1992), who found that the P inflow into hyphae of three arbuscular AM fungi reached a maximum after 4 weeks and then declined. This may be related to spore production initiated in *G. caledonium* after 3–4 weeks (unpublished observation).

In conclusion, the results from the present work indicate that the interactions between *F. candida* and the external mycelium of *G. caledonium* are limited. This is in contrast to the generally accepted hypothesis that mycophagous soil animals have a negative impact on the effectiveness of the AM symbiosis (Fitter and Garbaye 1994). Future studies on the interactions between AM fungi and Collembola will include other species of Collembola and isolates of AM fungi in order to determine whether Collembola–AM fungi compatibility is a crucial factor.

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