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Microarthropods influence the composition of rhizospheric fungal communities by stimulating specific taxa

Martina Janoušková[a,*], Petr Kohout[a,b,c], Jabbar Moradi[d], Pavla Doubková[a], Jan Frouz[d], Stanislav Vosolsobě[a,b], Jana Rydlová[a]

[a] Department of Mycorrhizal Symbioses, Institute of Botany of the Czech Academy of Sciences, Zámek 1, 25243, Průhonice, Czech Republic
[b] Department of Experimental Plant Biology, Faculty of Science, Charles University, Viničná 5, 12844, Praha 2, Czech Republic
[c] Laboratory of Environmental Microbiology, Institute of Microbiology of the Czech Academy of Sciences, Vídeňská 1083, 14220, Praha 4, Czech Republic
[d] Institute of Environmental Studies, Faculty of Science, Charles University, Benátská 2, 12800, Praha 2, Czech Republic

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ABSTRACT

It has been well established that grazing by fungivorous soil fauna alters competitive relationships among fungal species in simplified microcosmal conditions. To which extent fungal grazers modify the composition of complex fungal communities, however, remains little explored. We therefore addressed the question how microarthropods influence rhizospheric fungal communities and compared the effects of microarthropods among functional guilds of fungi as well as with those of the plant's mycorrhizal type, the key bottom up factor structuring microbial communities in the rhizosphere. In a greenhouse experiment, we cultivated *Tripleurospermum inodorum* (Asteraceae), a host plant for arbuscular mycorrhizal, and *Salix caprea*, an ectomycorrhizal host, or both hosts together in soil from a locality where both plants coexist. The defaunated soil contained its native fungal community while microarthropods were either left absent or re-introduced in two experimental treatments, combined in a factorial design with the three host plant treatments.

While only plant combination influenced the composition of the fungal communities by the main functional guilds (arbuscular mycorrhiza fungi, ectomycorrhizal fungi, endophytes, plant pathogens and saprotrophs), microarthropod presence had a significant effect on their taxonomic composition. Of the more abundant fungal genera (over 1% community share), microarthropods approximately doubled the relative abundances of five (*Cadophora*, *Exophiala*, *Truncatella*, *Meliniomyces*, *Trichosporon*), and significantly increased the absolute abundances of four. In contrast, only one genus (*Inocybe*) was significantly suppressed by the microarthropods. The genera belonged to all the main functional guilds except arbuscular mycorrhizal fungi. Tolerance to mechanical disturbance, dispersion in soil or response to low intensity grazing are suggested as mechanisms behind the observed stimulation of some fungal taxa.

1. Introduction

The overwhelming majority of soil fungi rely on plant-derived substances as food sources, and vegetation therefore constitutes a key factor in the bottom-up control of fungal communities (Taylor and Sinsabaugh, 2015). The presence and identity of living plants is especially important for communities of those fungal groups that form part of the root energy channel (Moore et al., 1988), i.e. mycorrhizal fungi, plant pathogens and endophytes (Peay et al., 2013; Bahram et al., 2016; Kolaříková et al., 2017). Within these groups, obligatory symbiotic arbuscular mycorrhizal fungi (AMF), most ectomycorrhizal fungi (EcMF) and plant pathogens ultimately depend in their growth on the presence of a host plant, while fungal endophytes, some EcMF and plant pathogens are to variable degree capable of saprotrophic growth (Smith and Read, 2008; Kohler et al., 2015; Kohout et al., 2018). Most other soil fungi are saprotrophs and rely on decomposition of dead plant material thus forming the detritus-based fungal energy channel (Moore et al., 1988). Their communities are directly influenced by litter characteristics such as C:N ratio or content of secondary metabolites (Urbanová et al., 2015), indirectly by interactions with the root-associated symbionts (Lindahl et al., 1999; Tiunov and Scheu, 2005).

Another important biotic interaction of soil fungi is with those soil-dwelling fauna that are specialized in the grazing of fungal mycelia - most prominently fungivorous nematodes, the microarthropods oribatids and collembolans, or larger arthropods such as isopods. Depending on their body size and density, they may exert significant

* Corresponding author.
E-mail address: martina.janouskova@ibot.cas.cz (M. Janoušková).

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feeding pressure and suppress fungal growth (Crowther and A'Bear, 2012; A'Bear et al., 2014) or, at low intensity of feeding, induce compensatory mycelial growth (Kampichler et al., 2004; Bretherton et al., 2006). Most importantly, fungal grazers display preferences for certain fungal species (e.g. Jorgensen et al., 2003; Schneider et al., 2005; Larsen et al., 2008; Koukol et al., 2009) or fungal groups, such as for dark pigmented mycelia over hyaline mycelia (Maraun et al., 1998a) or for saprotrophic fungi over AMF (Klironomos et al., 1999). Selective feeding pressure influences the outcome of competitive interactions among soil fungi (Sabatini et al., 2004; Crowther et al., 2011; A'Bear et al., 2013; Crowther et al., 2013; Kanters et al., 2015) and thus, fungivorous soil fauna potentially regulate the composition of fungal communities both at the level of functional groups and species. However, top-down control is traditionally assumed to play a negligible role in fungal assembly as compared to bottom-up factors (Wardle and Yeates, 1993).

Recently, Crowther et al. (2013) provided direct evidence for a classical top-down effect of isopod grazing on a dominant fungal taxon, which increased soil fungal diversity in microcosmal conditions. They argued that such top-down control of fungal communities is likely to be a wide-spread process. The potential to influence composition of fungal communities has been documented also for microarthropods, which exhibit a distinctly lower level of feeding pressure (A'Bear et al., 2014). They may accelerate fungal succession on litter (Klironomos et al., 1992; Maraun et al., 1998b), regulate the spread of fungal diseases (Sabatini et al., 2004), intensify competition among functional groups of soil fungi (Tiunov and Scheu, 2005) or modify the composition of litter-colonizing communities of EcMF (Kanters et al., 2015). These studies provided some insights into the effect of grazers on fungal communities in simplified conditions or within specific fungal groups. However, surprisingly little is known about the effects of grazers in complex systems colonized by a broad spectrum of functionally different fungal species. We ignore the relative importance of the faunal effects among functional guilds of fungi or in comparison to bottom-up factors.

The main aims of our study were therefore to determine the effects of microarthropod presence on functionally diverse fungal communities in the rhizosphere. More specifically, we compared the effects among functional guilds of fungi and with those of a major bottom-up factor shaping rhizospheric fungal communities – the plant's mycorrhizal host type. In a greenhouse experiment, soil containing a native fungal community was planted either with an AMF host plant species, an EcMF host or with both, and each system was cultivated either with or without a community of oribatids and collembolans. We assumed that the host plant treatment would importantly affect the communities of the corresponding mycorrhizal fungi, while the responses of the other guilds would be smaller. Within this frame, we expected to find distinct levels of response to the microarthropod presence among functionally different fungal groups. We anticipated the highest response for fungi of the detritus-based energy channel, i.e. saprotrophs, due to their dependence on the quality and quantity of soil detritus and corresponding niche differentiation.

2. Material and methods

2.1. Design, preparation and cultivation of the experiment

The experiment was established as two-factorial with host plant combination and presence/absence of microarthropods as factors. The three host plant combinations were as follows: (1) two individuals of the annual dicot *Tripleurospermum inodorum* (L.), (2) two seedlings of the tree *Salix caprea* L. and (3) combination of both host plants, each as one individual. *T. inodorum* is a highly mycorrhiza-responsive arbuscular mycorrhizal (AM) host plant, *S. caprea* is considered dual host of both AM and ectomycorrhiza (EcM). However, it forms predominantly EcM (Knoblochová et al., 2017; Kolaříková et al., 2017) and never formed AM in cultivation conditions similar to the experimental ones when cultivated without the presence of an AM host (unpublished results). The six combinations of the experimental factors were each established in five replicates, summing up to 30 pots in total.

The cultivation substrate originated from a large spoil bank of a brown-coal strip mine (Sokolov region, NW Bohemia, Czech Republic) composed of deposits of tertiary clays. The spoil bank has a long history of research on various aspects of ecological succession because it represents a mosaic of sites of successional stages differing in age. In the 30-year old succession stage, the original site of the substrate is dominated by *S. caprea* with sparse understory of predominantly AM grasses and herbs; the clay substrate is covered by a thick *S. caprea* litter layer, Oe fermentation horizon of 0.5–8 cm and a thin A horizon of 0.5 cm [see Rydlová et al. (2016) for more details on the substrate characteristics].

At the collection of the substrate, the litter layer was removed from the soil surface and the Oe fermentation horizon was collected separately from the predominantly mineral material underneath, which was excavated to the depth of about 30 cm, and each of the two substrate components was homogenized. Macro- and mesofauna was eliminated from the substrate components by two freezing/thawing cycles of 24 h at - 40 °C (Frouz et al., 2007), a procedure that largely preserves microfauna and microorganisms (Huhta et al., 1989). Defaunation by freezing produces some side effects on the physico-chemical and microbial properties of soils (Kampichler et al., 1999) and consequently, shifts in fungal community composition cannot be excluded. However, the microbial properties of the treated soils tended to recover within 20 days in previous studies (Wright et al., 1989; Stocum and Plante, 2006). The mineral substrate was filled into round plastic pots (700 ml volume), each equipped with a transparent plastic barrier heightening the pot's margin by 30 cm to keep microarthropods inside the pots. The fermentation horizon was placed as a layer of 1 cm on top of the mineral substrate in order to simulate, in a smaller scale, the soil layering at the site of soil origin.

Microarthropods were extracted from the fermentation layer, collected at the same site as the cultivation substrate, with a Berlese funnel apparatus with water as preservative fluid. On average, 80 g (dry weight) of fermentation layer was used for each funnel set up. The mounted funnels were emptied after 24 h and the extracted microarthropods were added to 15 of the 30 pots. The extractions were checked prior to the addition to the pots to remove any visible macrofauna. Three random extractions were used to estimate the average number of individuals of the two main microarthropod groups, collembolans and mites, added per pot, which were 90 and 160, respectively. These numbers correspond to average 8000 collembolans and 14,000 mites m^{-2}, which is in the range of microarthropod density at the site of soil origin (Moradi et al., 2017), taking into account the lower thickness of the fermentation layer in the experiment than at the field site.

Seeds of *S. caprea* were germinated in autoclaved sand for two month and transferred after germination to a seedling tray with 25-ml-cells filled with a 1:1 (v:v) mixture of autoclaved zeolite and non-sterile spoil bank substrate from the same site as the experimental substrate. After two weeks of greenhouse cultivation, seedlings of homogenous size were transplanted into the experimental pots. Seeds of *T. inodorum* were pre-germinated and subsequently cultivated in the same substrates as the *S. caprea* seedlings for 10 days before transplantation into the experiment simultaneously with the *S. caprea* seedlings.

The experiment was cultivated for 22 weeks (December to May) in a tempered greenhouse with temperature ranging between 10 °C (lowest night temperature) and 23 °C (highest day temperature towards the end of the cultivation period). Soil temperature was monitored and did not exceed 20 °C. The pots were watered according to the plants' needs, holes at the bottom of the pots, covered by fine mesh, prevented water accumulation in the pots.