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Soil biota effects on soil structure: Interactions between arbuscular mycorrhizal fungal mycelium and collembola

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ABSTRACT

Soil aggregation is an important ecosystem process mediated by soil organisms. Collembola and arbuscular mycorrhizal (AM) fungi are major soil biota representing different functional groups, and are known as two key promoters of soil aggregation. Although several studies have experimentally demonstrated that AM fungi and, more recently, collembola affect soil structure, there is no study investigating how both soil organisms affect soil aggregation excluding the influence of plant roots, another important driver of soil aggregation. Considering the importance of AM fungi and collembola in terrestrial ecosystems, here we asked if both organisms have any influence on soil aggregation when roots are not present.

In order to examine this question we conducted a completely factorial greenhouse study manipulating the presence of both collembola and AM fungi and excluded the roots of *Plantago lanceolata* using a 38 μm nylon screen compartment. We quantified soil aggregation as water stable soil aggregates in four size classes in the hyphal compartment and monitored a number of other explanatory variables, including AM (and non-AM) fungal soil hyphal length.

The soil in the hyphal compartment showed greater soil aggregation with larger mean weight diameter when collembola were present, and a similar result was found in the presence of AM fungi, compared to control treatments. Moreover, combined presence of both AM fungi and collembola resulted in a non-additive increase of soil aggregation.

Our study clearly indicated that collembola can enhance soil aggregation, that they can partially complement effects of AM fungi, and that these effects are independent of roots.

1. Introduction

Soil structure, as the three dimensional matrix of pore and solid spaces, is an ecosystem property essential for facilitating water and gas exchange, carbon storage, nutrient cycling, resistance to erosion and other functions (e.g., Six et al., 2000; Coleman et al., 2004). Soil aggregation, the process leading to soil structure, is thus a principal ecosystem process, which can be directly or indirectly controlled by various soil biota in a given environmental setting (e.g. soil organic matter, texture, climate) (Bronick and Lal, 2005; Rillig and Mummey, 2006).

Aggregation of soil is the result of various binding agents, where plant roots and fungal hyphae play an important role, in particular for macroaggregates (>250 μm) (Tisdall and Oades, 1982), as opposed to microaggregates, which are stabilized by more permanent binding agents. Indeed, several studies have highlighted the important contribution of arbuscular mycorrhizal (AM) fungi to soil aggregation (Miller and Jastrow, 1990; Jastrow and Miller, 1998; Jastrow et al., 1998; Rillig and Mummey, 2006). AM fungi are considered a key functional component in the soil (Rillig, 2004; Smith and Read, 2008), serving as an important link within the plant–soil continuum (Wilson et al., 2009), and are recognized as key promoters of soil aggregation (Piotrowski et al., 2004; Rillig and Mummey, 2006; Chaudhary et al., 2009). The evidence for AM fungal contribution to soil aggregation is strong, as provided by a wide range of field observational studies (Rillig et al., 2002a, b), field experiments (Wilson et al., 2009), mechanistic greenhouse experiments (Thomas et al., 1993; Bearden and Petersen, 2000; Piotrowski et al., 2004; Hallett et al., 2009; Bedini et al., 2009), and more recently, by tests with exclusion of all other biota (Rillig et al., 2010).

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By comparison, a lot less direct experimental data exists for soil animals in regard to soil aggregation, with the exception of earthworms, which are well-documented in their effects on soil structure (Bossuyt et al., 2005, 2006; Davidson and Grieve, 2006; Kavdir and İlay, 2011). Soil microarthropods, in particular collembola, are ubiquitous soil animals (Petersen and Luxton, 1982) and can influence a range of ecosystem processes (e.g., Finlay, 1985; Wardle and Bardgett, 2004). Lussenhop (1992) hypothesized that collembola could contribute to soil aggregation through their fecal pellets, which are typically 30–90 μm in diameter (Rusek, 1975). Recently, studies in our lab have provided the first direct experimental evidence that collembola are capable of enhancing soil macroaggregation (Caruso et al., 2011; Siddiky et al., 2012). In these studies, the combined presence of collembola and AM fungi led to a higher level of macroaggregation than the individual effects of collembola or AM fungal presence, which also individually significantly enhanced soil aggregation (Siddiky et al., 2012). These previous greenhouse studies were conducted in the presence of plant root systems, i.e. plant roots were not experimentally isolated from the added AM fungi or collembola. Thus it is not clear to what extent the observed positive responses in soil aggregation to AM fungi, collembola or their combination were mediated by indirect effects via the roots.

Roots are widely appreciated agents of soil aggregation (Tisdall and Oades, 1982; Miller and Jastrow, 1990; Jastrow et al., 1998; Rasse et al., 2000; Six et al., 2004). Entanglement of soil particles by roots may directly promote macroaggregates (Tisdall and Oades, 1982; Miller and Jastrow, 1990; Jastrow et al., 1998). Moreover, roots contribute to soil aggregate stabilization by releasing organic materials (e.g., rhizodeposition), serving as aggregate binding agents (Morel et al., 1991). Moreover, roots can also indirectly influence soil aggregation through alteration of microbial communities (Morel et al., 1991) or modification of the soil water status (Reid and Goss, 1982). A number of studies (e.g., Monroe and Kladivko, 1987; Materechera et al., 1994) also reported that the penetration of roots into macropores can result in a decrease of macroaggregates (up to 50%). Irrespective of the mechanism(s) involved, effects of roots, and their possible interactions with the biota under investigation, need to be excluded in any attempt to isolate effects of AM fungi or collembola.

Nevertheless, few previous studies have tried to experimentally separate the influence of AM fungal hyphae and their host plant roots on soil aggregation (e.g., Thomas et al., 1993; Bearden and Petersen, 2000; Hallett et al., 2009). To disentangle the influence of AM fungal hyphae and collembola on soil aggregation from the effects of plant roots, in the present study we excluded the roots by using a screen that permits only the passage of AM fungal hyphae. We hypothesized that in the absence of plant root effects, collembola would reduce AM fungal abundance, and therefore would indirectly lead to a decrease in soil aggregation. However, in addition to these indirect effects, collembola may have direct positive effects on soil aggregation. In order to test these hypotheses, we conducted a factorial greenhouse experiment manipulating the presence of both AM fungi and collembola in a volume of soil from which roots were excluded.

2. Materials and methods

2.1. Experimental design and greenhouse experiment

We conducted a 2 × 2 factorial greenhouse experiment where ten replicates were set up for each combination of the four treatments, Collembola (present, absent) and AM fungi (present, absent), with a total of 40 experimental units (pots); the full, balanced factorial design allowed us to test for two effects and their interactions.

We used a sandy soil collected from an experimental field of Freie Universität Berlin. The site is a meadow, and the soil an Albic Luvisol. The soil properties were: sand = 74%, silt = 18% and clay = 8%; 6.9 mg/100 g P (calcium–acetate–lactate); 5.0 mg/100 g K (calcium–acetate–lactate); 0.12% N (total); 1.87% C (total) (analyses conducted by LUFA Rostock Agricultural Analysis and Research Institute, Germany; and using an Euro EA C/N analyzer, HEKAtech GmbH, Wegberg, Germany). The soil was chosen due to its high mycorrhizal inoculum potential and general responsiveness to biota in terms of soil aggregation (Rillig et al., 2010). Soil was sieved (10 mm) prior to use to remove stones and roots. In order to reduce soil fertility, the soil was thoroughly mixed with sand (70% soil with 30% sand). Following that, the soil was steamed at 90 °C (4 h) to eliminate AM fungi and collembola.

Pots (4 L) were divided in two compartments as shown in Fig. 1. The compartments were set up using a solid round mesh tube (height 20 cm; diameter 7 cm) made of 0.5 mm aluminum net (supplied by: BAHAG AG, Bauhaus Handelsges., D-68167 Mannheim, Germany) covered with a 38 μm plastic screen (obtained from: SEFAR AG, CH-9410 Heiden, Switzerland). The screened tube was open at the top to allow the plant to grow within. This mesh size allows only the passage of AM fungal hyphae between compartments, but not of roots. The outer compartment is designated as hyphal compartment. We closed the bottom of mesh tubes with plastic tape (2 mm thickness) and sealed with silicon (supplied by BAHAG AG, Bauhaus Handelsges., D-68167 Mannheim, Germany) to prevent plant roots from penetrating the hyphal compartment during the experiment. The inner compartment is

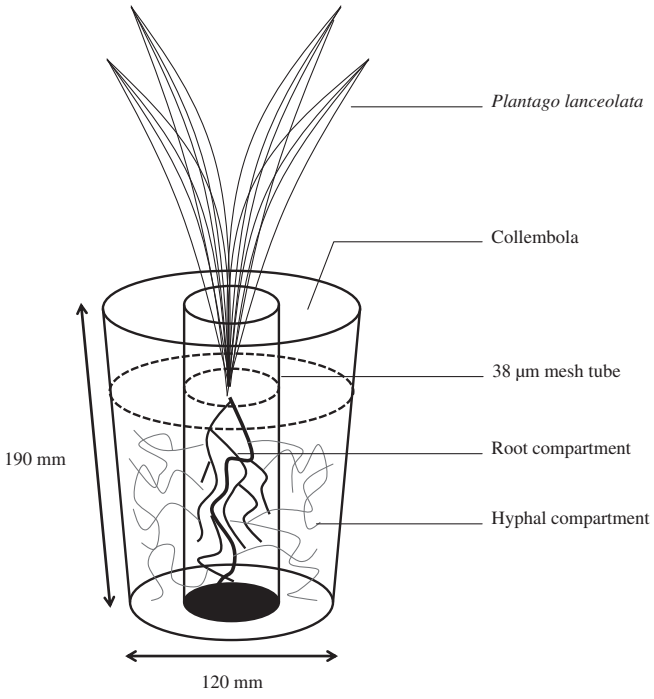

Fig. 1. Schematic representation of root compartment set vertically in the center in each experimental unit (pot). Each compartment was open at the top to receive a plant, the side wall was covered by a 38 μm nylon mesh, and the bottom was closed with plastic tape sealed with silicone. Inside the compartment, a plant grows inoculated or not with AM fungi, while outside there was addition or not of collembola. The 38 μm mesh prevents the roots (which have larger diameters) from growing outside the comportment, allowing only the AM fungal mycelium to grow into the hyphal compartment. The rim of the hyphal compartment (height from soil surface: 10 cm) prevented collembola from entering the root compartment.