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Arbuscular mycorrhizal fungi reduce decomposition of woody plant litter while increasing soil aggregation

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ABSTRACT

The decomposition of plant organic matter and the stability of soil aggregates are important components of soil carbon cycling, and the relationship between decomposition rate and arbuscular mycorrhizal fungi (AMF) has recently received considerable attention. The interaction of AMF with their associated microorganisms and the consequences for litter decomposition and soil aggregation still remain fairly unclear. In a laboratory pot experiment we simultaneously tested the single and combined effects of one AMF species (*Rhizophagus irregularis*) and a natural non-AMF microbial community on the decomposition of small wooden sticks and on soil aggregation. To disentangle effects of hyphae and roots we placed mesh bags as root exclusion compartments in the soil. The decomposition of the wooden sticks in this compartment was significantly reduced in the presence of AMF, but not with the non-AMF microbial community only, compared to the control, while aggregation was increased in all treatments compared to the control. We suggest that AMF directly (via localized nutrient removal or altered moisture conditions) or indirectly (by providing an alternative carbon source) inhibited the activity of decomposers, leading to different levels of plant litter degradation under our experimental settings. Reduced decomposition of woody litter in presence of AMF can be important for nutrient cycling in AMF-dominated forests and in the case of woody plants and perennials that develop lignified roots in grasslands.

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1. Introduction

The decomposition of plant litter in soil is a key ecological process and can be an important factor determining soil carbon (C) storage. Since two thirds of the earth's carbon are stored in terrestrial ecosystems (Jobbagy and Jackson, 2000; Amundson, 2001) the storage of soil C is a key component of the global carbon cycle, and because arbuscular mycorrhizal fungi (AMF) have been shown to affect litter decomposition they could have an important influence on this process (e.g. Cheng et al., 2012; Herman et al., 2012; Drigo et al., 2013). Until recently AMF were thought to contribute to soil C storage mainly through channeling plant photosynthates into soil and contributing to stabilization of C within soil aggregates (Six et al., 2004; Talbot et al., 2008). However, this potentially positive effect on soil C levels can be offset if AMF simultaneously promote decomposition of plant litter: even though AMF do not have saprotrophic capabilities, they can enhance decomposition of organic matter (OM) (Hodge et al., 2001; Koller et al., 2013). Indeed, Cheng et al. (2012) showed that plant litter decomposed faster in the presence of AMF, especially under conditions of elevated CO_2 and nitrogen (N) concentrations. Likewise, Hodge et al. (2001) have shown an increased plant capture of N from a patch containing leaf litter, simultaneously with a reduction of C in the patch, in the presence of AMF, and hypothesized that AMF promoted decomposition by stimulating the activity of hyphosphere bacteria.

Meanwhile, there are also studies that indicate that soil carbon levels do not necessarily decrease in response to AMF: a long-term field study (17 and 6 years) found carbon stocks to positively correlate with AMF extraradical hyphae (Wilson et al., 2009), and a mesocosm experiment found AMF root colonization to positively associate with the amount of stable soil C (Manning et al., 2006). One potential reason for the observation that AMF do not decrease soil C levels could be that they differentially affect plant litter

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depending on litter quality: litter can be slowly or fast decomposing depending on its chemical constitution (Milcu et al., 2011; Cotrufo et al., 2013). Slowly decomposing litter such as lignified plant material is a major contributor to soil OM and its decomposition depends on a number of factors including humidity, size/shape of wood particles and the organisms involved (Boddy and Watkinson, 1995). In the soil environment fungi are the main decomposers of woody litter and the relationship between numerous saprotrophic fungi and wood decomposition has been studied intensively (e.g. Boddy and Watkinson, 1995; Worrall et al., 1997; Clinton et al., 2009). However, to our knowledge the effect of AMF on decomposition of woody material has not yet been studied, even though lignified plant roots, stems and leaves can represent a considerate proportion of litter in many natural ecosystems (Heim and Schmidt, 2007).

As mentioned before, another way by which AMF may affect soil C cycling is through their effects on soil structure, i.e. the size and distribution of soil aggregates and pores, which determines nutrient and water availability, oxygen diffusion and relations of predator and prey (Rillig and Mummey, 2006). OM can be further physically protected within soil aggregates and thus a higher soil aggregate stability can contribute to OM stabilization in the soil (reviewed in Six et al., 2004). The role of AMF in soil aggregate formation and stabilization is well documented (see review of Rillig and Mummey, 2006) and we recently showed in a meta-analysis, using a wide range of studies, that AMF generally increase soil aggregation (Leifheit et al., 2014).

While it is clear that AM fungi are important for soil aggregation, they are usually part of a wider natural microbial community with numerous organism interactions, i.e. bacteria and non-AM fungi can also play an important role in soil aggregation (Tisdall, 1994) and litter decomposition (Hodge et al., 2001). Rillig et al. (2005) showed that various AMF species differentially affect microbial community composition and that these differences are important for soil aggregation. Furthermore, the combination of fungal species and host plant, the characteristics of the fungal species and the soil microbial community composition can strongly influence the effects of AMF on soil aggregation (Schreiner et al., 1997; Piotrowski et al., 2004). Given that AMF affect litter decomposition indirectly through their effects on decomposers, e.g. by imposing N limitation or altering rhizodeposition and thereby altering the C supply to other microorganisms (Cheng et al., 2012; Nuccio et al., 2013), the composition of the microbial community present may also be expected to determine the effect of AMF on litter decomposition rate.

In this study we aim to assess how AMF and other soil microorganisms interact to affect 1) woody litter decomposition and 2) soil aggregation. Therefore we tested whether the decomposition of small wood pieces would be influenced by the presence of AMF, while excluding effects of plant roots, and if potential effects would be enhanced or reduced by the presence of a more natural microbial assemblage. For soil aggregation we expected a positive, additive effect of AMF and associated microorganisms as both groups are capable of forming and stabilizing soil aggregates.

2. Materials and methods

2.1. Experimental design and setup

In a 2×2 factorial experiment we tested for the effects of presence/absence of AMF and a natural microbial community and the interaction between these two factors. Each treatment combination was replicated 10 times for a total of 40 pots. The experiment was located in a climate chamber with an average day/night temperature of 20/16 °C. The soil was a loamy sand collected from an experimental field of Freie Universität Berlin, which had the following properties: pH 7.1 ($CaCl_2$), 6.9 mg P/100 g soil (calcium-acetate-lactate), 0.12% N (total) and 1.87% C (total) (for analytical methods see Rillig et al. (2010)). The vegetation at the field site is dominated by grassland species (*Trifolium repens* L., *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl, *Bellis perennis* L., *Plantago lanceolata* L., *Elymus repens* L. Gould, *Medicago sativa* L.) with a few cherry trees (*Prunus* spec.) at the borders. The soil was autoclaved twice on two consecutive days with at least 24 h in between in order to ensure absence of viable microbial propagules. The soil was dried in the autoclaving bags at 60 °C and subsequently broken up with a rubber mallet to reduce soil aggregation. The soil was then sieved using a 2 mm sterilized sieve and simultaneously mixed with 20% autoclaved sand in order to partially compensate for nutrient release during sterilization, resulting in a sand content of 79%. One and a half liters of the soil-sand-mixture were transferred into 3 L round plastic pots with a 2 cm layer of sterilized sand on the bottom and on the top. Close to the center of the pot a mesh bag (120 ml volume, 38 μm pore size) was installed to allow the penetration of hyphae and the passage of bacteria while excluding roots (hereafter referred to as root exclusion compartment). The top of the mesh bags was left open and was positioned above the soil surface (see Fig. S1, Supplementary Material). Pots were re-randomized regularly throughout the experiment.

Seeds of *P. lanceolata* (a perennial mycorrhizal rosette forming herb of grasslands, ruderal areas and farmland) were sterilized in 10% bleach for 10 min and in 70% ethanol for 30 s, rinsed in deionized water after each step, and sown directly into the soil. After seedling emergence plants were thinned to one plant per pot (further referred to as root compartment). During the growing period plant leaves were cut twice to a height of approximately 15 cm to prevent excessive growth of leaves (to avoid contamination from neighboring pots) and roots (to avoid pot bound roots). Plants were watered as needed three times per week. We used *P. lanceolata* as plant species because it is common in the grassland where the soil for the experiment was collected.

Control pots were left non-inoculated. For the AMF treatment we inoculated approximately 1000 spores per pot of *Rhizophagus irregularis*, a member of the Glomeraceae family and frequently referred to as “the model AMF” (Stockinger et al., 2009) and a very commonly encountered AMF species in temperate Europe and commonly used in mycorrhizal research (Öpik et al., 2010; Moora et al., 2011) (Schenk & Smith, isolate DAOM197198, Symplanta GmbH & Co. KG). The sterile spores were contained (pre-mixed) in a rock flour material (attapulgit clay based powder) that was mixed with deionized water and pipetted into a cut-off pipette tip that was positioned under the plant towards the roots. The controls received sterilized carrier material. Fresh field soil from the uppermost 30 cm, collected at the same field site as above, was used to produce a microbial wash from a soil filtrate (200 g of soil in 2 L of tap water) where the smallest sieve had a size of 20 μm, thus excluding larger spores such as those of AMF. This microbial wash represents the non-AMF microbial community. We inoculated the microbial wash (‘MW’) to the seedlings of the treatments and autoclaved microbial wash to controls. Inoculation with both AMF and MW will later be referred to as the ‘AMF + MW’ treatment.

To measure microbially mediated decomposition we used wooden sticks that were inserted in the soil and determined their mass loss rate at the end of the experiment (Sinsabaugh et al., 1993; Arroita et al., 2012). The wooden sticks (4 × 2 mm width, Meyer & Weigand GmbH, Germany) were cut into pieces of ca. 30 mm length, autoclaved and weighed (154.43 mg ± 0.35, $N = 30$). We used a *Tilia* species, which is a common tree in the surrounding of the field site where the soil was collected. One stick was introduced into the soil of each compartment (root exclusion and root compartment) using a spatula. Each stick contained approximately

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