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Effect of water redistribution by two distinct saprotrophic fungi on carbon mineralization and nitrogen translocation in dry soil

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ABSTRACT

Hydraulic redistribution (HR) of water from wet to dry soil compartments by non-differentiated mycelium was recently shown for the saprotrophic fungus *Agaricus bisporus*. The redistributed water triggered the carbon (C) mineralization in the dry soil. The potential of other saprotrophic fungal species and their mycelia networks for HR in soils is unknown. Here, we tested the potential for HR of the mycelial cord forming species *Schizophyllum commune*, compared it to capillary water transport in a sandy soil and assessed the impact of HR on C mineralization and enzyme activities in mesocosm experiments with dry and wet soil compartments using labeled water (^{2}H) and labeled organic substrate (^{13}C, ^{15}N). Further, we determined nitrogen (N) translocation between the soil compartments by the mycelium of *S. commune* and *A. bisporus*. The flow velocity of redistributed water in single hyphae of *S. commune* was about 0.43 cm min^{-1} which is 1.5–2 times higher than in hyphae of *A. bisporus*, suggesting that cords enhance fungal HR. The amount of redistributed water was similar to capillary transport in the sterile sandy soil. Despite greater potential for HR, *S. commune* only slightly increased C mineralization and enzyme activity in the dry soil within 7 days. *S. commune* translocated N towards the organic substrate in the dry soil and used it for hyphal growth whereas *A. bisporus* redistributed N within the mycelial network towards the wet soil. Our results suggest that fungal hyphae have the potential to overcome capillary barriers between dry and wet soil compartments via HR and that the impact of fungal HR on C mineralization and N translocation is related to the foraging strategy and the resource usage of the fungus species.

1. Introduction

Periods of drought and the resulting soil desiccation are important abiotic stressors negatively affecting soil organisms and ecosystems (Schimel et al., 2007). Low water potentials lead to a limitation, or under extreme conditions, even to a total inhibition of microbial activity in soils (Borken and Matzner, 2009; Manzoni et al., 2012). Drought stress can also alter microbial community composition, with fungal communities in non-tropical climate systems usually being less sensitive and better adapted compared to bacterial communities (Bapiri et al., 2010; Sheik et al., 2011; Yuste et al., 2011; Allison et al., 2013; Alster et al., 2013).

A shift of the bacteria to fungi ratio in soils due to water stress results from the need of many bacteria for a constant water supply (Greenwood, 1967). The potential of mycelia networks for hydraulic redistribution (HR), i.e., water transport along soil water potential gradients, might be a mechanism for the higher resistance of some fungi to drought. HR from wet to dry soil compartments has been shown for plant roots and mycelia networks of mycorrhizal fungi as well as for a saprotrophic fungus (Thompson et al., 1985; Jennings, 1987; Dawson, 1993; Querejeta et al., 2003; Guhr et al., 2015). The redistributed water in hyphae and roots can increase the water content in the soil by leakage from root or hyphal tips (Querejeta et al., 2003; Domec et al., 2004). Further, as recently shown for the saprotrophic fungus *Agaricus bisporus* (Lange) Imbach, HR by non-differentiated mycelium can enhance extracellular enzyme activity and the mineralization of soil organic matter in dry soil (Guhr et al., 2015).

It is, however, not clear if HR is a general trait of saprotrophic fungi and how the redistributed water is used by the fungi. The translocation of water and nutrients is known to vary among fungal species with different foraging strategies (Cairney, 1992, 2005). The same may hold true for the effect of HR on organic matter mineralization.

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Filamentous fungi have developed different foraging strategies by differentiation of mycelia network organizations. Some species only expend by radial growth of hyphae while others form complex mycelial network organizations like mycelial cords, i.e., aggregations of predominantly parallel and longitudinally aligned hyphae, and rhizomorphs (Boddy, 1999). The translocation of nutrients and water is more effective in mycelial cords and rhizomorphs than in non-differentiated mycelium (e.g., Lindahl et al., 2001; Cairney, 2005; Watkinson et al., 2006). Distances for nutrient translocation in fungal cords can be > 1 m (Boddy, 1993) and translocation velocity can be > 25 cm h^{-1} in cords (Wells and Boddy, 1990). Therefore, fungal cords and rhizomorphs are considered as "highways" for water and nutrient transport in soils (e.g., Jennings, 1987; Cairney, 2005). As with nutrient translocation, HR through fungal cords is probably more effective than through single hyphae.

The interaction of HR by mycelia networks and N translocation is yet unknown. In general, transport of nutrients and water in hyphae can occur bi-directionally, either towards the growing front or towards the base of the mycelial network (Cairney, 1992). The transport is generally considered to occur from sources to sinks (Lindahl et al., 2001). Therefore, nutrients are mainly translocated from nutrient sources at the growing front towards the base (Cairney, 1992). However, transfer of nutrients can also occur towards the growing front supporting the production of biomass (Jennings, 1987; Olsson and Gray, 1998; Tlalka et al., 2003). Further, saprotrophic fungi that decompose substrates with high C:N ratios are known to translocate N towards new C sources (Boberg et al., 2014; Frey et al., 2000; Tlalka et al., 2002). Thus, the fungal foraging strategy may have an effect on the amount and direction of N translocation within the mycelia network (Watkinson et al., 2006).

A saprotrophic fungal species of interest for studying HR by fungi is *Schizophyllum commune* Fries, as this species has the ability to form mycelial cords (Balaş and Tănase, 2012). *S. commune* is one of the most widespread fungi on earth (Ohm et al., 2010), adapted to substrates with high C:N ratios and known as a wood decomposing fungus causing white rot in woody debris (Schmidt and Liese, 1980). Additionally, *S. commune* grows on aboveground litter (Olsson and Gray, 1998; Seephueak et al., 2011), dead roots (Zhang et al., 2009; Glen et al., 2014) and was also found in mineral soils (Varghese, 1972; Neuhauser et al., 2009). Its genome includes a high number of genes coding for enzymes needed for degradation of lignocellulosic compounds (Ohm et al., 2010). The wide distribution and the high potential for decomposition of plant derived lignocellulosic components makes this species a suitable candidate for studying HR and nutrient translocation.

Here, we measured water translocation rates by HR of *S. commune* and compared the rates to capillary transport of a sandy soil. We further analyzed the impact of HR by *S. commune* on C mineralization and enzyme activities in dry soil-litter systems. Furthermore, we assessed the translocation of N within the mycelia networks of *S. commune* and *A. bisporus* in a mesocosm system with a strong gradient in soil water potential.

2. Materials & methods

2.1. Experimental setup

Experiments were carried out in mesocosms as described in Guhr et al. (2015). Briefly, mesocosms consisted of 2-chamber units (6 × 20 × 15 cm) filled with a homogenized and steam sterilized mineral soil (2:1:1 v/v/v mixture of loamy soil (17% clay; 76% silt; 7% sand), medium coarse quartz sand (Dorsilit 8, particle size range: 0.3–0.8 mm) and coarse quartz sand (Dorsilit 7, 0.6–1.2 mm, both Dorfner GmbH & Co., Hirschau, Germany). The bulk density of the soil was adjusted to 1.33 g cm^{-3}. Soil hydraulic parameters according to the van Genuchten model (with m = 1-1/n; Van Genuchten et al., 1991) were: residual water content = 0.078 m^3; m^{-3}; saturation water content = 0.41 m^3 m^{-3}; saturated hydraulic conductivity = 3.83 cm day^{-1}. The chambers of a mesocosm were separated by a 2 mm air gap (hydraulic barrier) to prevent capillary water flow. The air gap was stabilized by 2 stainless steel mesh screens on each side (pore-size: 160 μm).

Soil of chamber I was inoculated with *S. commune* (provided by the Department of Mycology at the University of Bayreuth) or *A. bisporus* (DSM No. 3056, from the Leibniz Institute DSMZ) by placing a 1 cm^2 agar plate with fungal hyphae close to the air gap at approx. 2 cm depth. The mesocosms were maintained at 23 °C and irrigated regularly to field capacity with a liquid fungal growth medium (2% glucose, 0.2% peptone, 0.2% yeast extract, 0.1% K_2HPO_4, 0.46% KH_2PO_4, and 0.05% $MgSO_4$, Nazrul and YinBing, 2011) for 6 weeks to generate hyphal growth in both chambers. Afterwards, the soil of all mesocosms (both chambers) was desiccated for 6–8 weeks to a soil water potential of about −9.5 MPa. Volumetric water contents were measured continuously using soil moisture sensors (ECH_2O-10 moisture sensor, Decagon Devices Inc., Pullman WA, U.S.A.).

After desiccation, only chamber I was rewetted to field capacity (−0.03 MPa) while chamber II of each unit remained dry. These water potentials (−0.03 MPa and −9.5 MPa) were adjusted to achieve a strong water potential gradient between the chambers at moderate water stress for the fungi (cf. Dix, 1984; Manzoni et al., 2012). The number of hyphae bridging the air gap was estimated after each experiment by counting hyphae in 10 randomly chosen openings on the mesh screen. The mean value of all counts was then extrapolated to the whole area of the air gap (25 openings per cm^2, cross-sectional area of all openings at the soil contact area: 47.1 cm^2). Further, all visible cords were counted as well.

Two experiments were conducted with both fungi to quantify (I) HR (n = 4 for each species), and (II) C mineralization and N translocation (n = 5 *A. bisporus*; n = 6 *S. commune*) between the chambers of the mesocosms. In the controls (n = 4–6 as in the treatments, respectively), HR was prevented by cutting the hyphal bridges between the 2 chambers with a thin stainless-steel wire prior to rewetting. Additionally, 2 non-inoculated mesocosms without fungal hyphae were prepared to measure capillary water transport from chamber I to chamber II along the water potential gradient. These mesocosms had no air gaps or mesh screens and were filled throughout with homogenized mineral soil.

2.2. Quantification of HR

To quantify HR and capillary water transport, chamber I was rewetted with deuterium-labeled water (3 atom% deuterium enrichment, ROTH GmbH + Co. KG, Karlsruhe, Germany). Mesocosms were then closed air-tight and only opened for destructive sampling of soil cores from chamber II 72 h after irrigation of chamber I. About 50 g soil dry weight was taken at each of 3 distance points from the air gap (5, 10 and 15 cm). Soil water potential was measured using the dewpoint method (WP4-T, Decagon Devices Inc., Pullman WA, U.S.A.). Water for deuterium analysis was extracted by cryogenic vacuum extraction. Deuterium analyses were conducted at the Laboratory for Isotopic-Biogeochemistry (University of Bayreuth) using thermal conversion/isotope-ratio mass-spectrometry (TC-IRMS; IRMS: delta V advantage, Thermo Fisher Scientific, Bremen, Germany; pyrolysis oven: TG pyrolysis oven HTO, HEKAtech, Wegberg, Germany; interface: ConFlo IV, Thermo Fisher Scientific, Bremen, Germany). Values are reported in conventional delta notation, defined as ‰ deviation from a reference standard (VSMOW: Vienna standard mean ocean water). The