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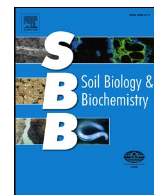

Soil microbial food web channels associated with biological soil crusts in desertification restoration: The carbon flow from microbes to nematodes

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ABSTRACT

Development from bare soil to biological soil crust (BSC) after the establishment of vegetation for sand fixation is an important desertification rehabilitation process in dryland ecosystems. While subsequent changes aboveground have been well documented, few studies focused on how BSC affects soil food webs after vegetation establishment. In this study, we investigated how soil food web channels respond to BSC, and in particular how flow of carbon from microbes to higher trophic levels is affected in Horqin Sandy Land, China. The BSC layer and 0–1 cm depth soil layer without BSC (as the control of BSC) were taken. After that, soil samples of 10 cm depth were collected and then dividing into two equal 5 cm parts for comparing soil microbe and nematode community composition in 2013 and 2014. The results showed that presence of BSC increased the phospholipid fatty acid and biomass carbon of microbes in the top layer of both years. Abundance, biomass carbon, and metabolic footprint of nematode trophic groups, including fungivores and omnivores-predators in the top layer, had higher values under BSC. Positive relationships were found between total organic carbon of BSC and biomass carbon of fungi, and between biomass carbon of fungi and fungivores. BSC enhanced carbon flow from fungi to fungivores, with higher connectance values in the fungal channel than in soil without BSC. The strengthened relationships between total organic carbon of BSC and omnivore-predator, and high connectances of the fungal channel and of the omnivore-predator channel under BSC, suggest a more reticulated channel in soil food web. It can be concluded that colonization of BSC enhances the connenctances in soil microbial food web channels, and could contribute to the resilience of dryland ecosystems.

1. Introduction

Drylands constitute over 40% of the world's terrestrial land mass and hold an estimated 25% of global soil organic carbon (Safriel and Adeel, 2005; Belnap, 2006).

Biological soil crust (BSC) is a fundamental component of drylands worldwide, and it constitutes up to 70% of the living cover of dryland soils (Ferrenberg et al., 2015). It colonizes and gradually develops after establishment of sand-binding vegetation (Li et al., 2010). Cyanobacteria, algae, fungi, lichen and moss are the mainly components of BSC, providing diverse ecological functions (Bowker et al., 2010). BSC greatly affects carbon and nitrogen fixation (Bowker et al., 2011; Yan-Gui et al., 2011), land stabilization (Belnap and Gillette, 1998), hydrological cycle regulation (Belnap, 2006), and biodiversity maintenance (Darby et al., 2010) in dryland ecosystems. Therefore, a clear understanding of the ecological function of BSC is important to the management and control of desertification in dryland ecosystems (Belnap, 2006; Chamizo et al., 2012). Although the influence of BSC on soil abiotic properties has been well documented, the relationships between BSC and the soil food web remain poorly understood (Housman et al., 2007; Delgado-Baquerizo et al., 2013).

Soil food webs deliver important ecological functions, such as organic matter decomposition and nutrient cycling, which are necessary to belowground processes in desertification restoration (Wall and Virginia, 1999; Sánchez-Moreno and Ferris, 2007). Here we focus on the micro-food web (Wardle, 1995; Niwa et al., 2011; Li et al., 2012a), which includes microorganisms (bacteria and fungi), microbivorous nematodes (bacterivores and fungivores), and predatory nematodes (omnivores-predators). Two main food web pathways are presumed to account for carbon fluxes through most soil food webs: (1) the detritus

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pathway, which includes the bacterial channel and the fungal channel, and (2) the root channel (Moore et al., 2004; Sánchez-Moreno et al., 2011). There is growing evidence that these channels are intimately linked, especially by omnivores that feed across multiple trophic resources (Rooney et al., 2006; Wolkovich et al., 2014) and which therefore can couple "separate" channels (Wolkovich, 2016), making them particularly influential for the regulation of the soil food web (Moore and Hunt, 1988).

Soil nematodes are ubiquitous inhabitants of soil ecosystems and occupy a central position in soil micro food webs (Pen-Mouratov et al., 2003; Yeates, 2003). They are also good indicators for evaluating soil food web structure and function (Neher, 2001; Wasilewska, 2006). Previous studies have shown that nematode communities develop in parallel to BSCs development (Darby et al., 2007; Liu et al., 2011), and therefore nematodes could be used as indicators of BSC development (Zhi et al., 2009; Wildemeersch et al., 2015). Through their effects on the soil microbial community, nematodes support many ecological functions and services in arid and semi-arid ecosystems (Wall et al., 2002; Pen-Mouratov et al., 2011), but their responses to BSC formation and corresponding effects on the soil food web channels are not clearly understood. In recent years, Ferris (2010) introduced the nematode metabolic footprint (NMF) concept, which allows a functional quantification of biomass, metabolic activity and magnitude of carbon and energy flow in the soil food web (Ferris et al., 2012; Bhusal et al., 2015; Zhang et al., 2015b). The metabolic footprints of nematodes, based on carbon utilization in production and respiration, could provide information about the responses of soil food web to resources and their contribution to ecosystem functions and services (Ferris et al., 2012; Zhang et al., 2012).

The objectives of this study were to reveal how BSC development in a semi-arid area affects soil food web channels and carbon flow through the microbial food web. We tested the following hypotheses. First, presence of BSC would have positive effect on abundance of soil microbes and nematodes. Second, presence of BSC would increase the metabolic activities of soil organisms, here investigated by estimation of metabolic footprints. Third, the carbon flow from soil microbes to nematodes would be enhanced by BSC.

2. Material and methods

2.1. Study site

This study was conducted at the Wulanaodu Experimental Station of Desertification (43°02′N, 119°39′E), Institute of Applied Ecology, Chinese Academy of Sciences. The station is located in the western Horqin Sandy Land of Northeast China. Annual mean air temperature is 6.3 °C, and annual mean precipitation is 340 mm, approximately 70% of which falls between June and August. The annual mean wind velocity ranges from 3.2 to 4.5 m s^{-1}. The soils are classified as Cambic Arenosols (IUSS, 2006). The landscape is characterized by drifting, semi drifting and stabilized sandy lands (Jiang et al., 2007). Sand dune movement, wind erosion, and sand burial are frequent in this area. Indigenous perennial shrubs (*Caragana microphylla* Lam.) were planted on active sand lands with the help of straw checkerboards (1 × 1 m^2 squares) as sand binders in order to prevent desertification since 1984. Straw was arranged in belts and the orientation of the belts was perpendicular to the prevailing wind direction (Su and Zhao, 2003; Cao et al., 2008). After over 30 years of restoration, BSC formed and included abundant moss crust composed of *Didymodon constricuts and Bryum argenteum.*

2.2. Experimental design and sampling

Soil was sampled on August 24th, 2013, and June 4th, 2014. Four 10 × 10 m^2 plots were selected randomly as replicates in sandy land that had experienced vegetation restoration since 1984. The distance between each neighboring plot was no less than 10 m. In each plot, a replicate sample with BSC and one without BSC (NBSC) were collected, each a composite soil sample of five randomly located sampling points. Before excavation, BSC layers of about 1 cm thickness above the soil were collected in plastic petri dishes; for the samples without BSC (NBSC), soils at the 0–1 cm depth were collected. Hereafter both the BSC layer and 0–1 cm layer of NBSC are referred to as the O layer. Then, soil samples to 10 cm depth beneath the O layer were collected using a shovel, and then divided into two equal parts, the top 5 cm (A layer) and the bottom 5 cm layer (B layer). There were 32 composite samples in total, 4 replicates × 2 depths (A and B layers) × BSC/NBSC × 2 sampling years, each about 1000 g. Large roots and other debris were removed. All samples were put into individual plastic bags and were kept at 4 °C until further analyses.

2.3. Analysis of soil physicochemical properties

Soil moisture (SM) was determined gravimetrically by drying samples at 105 °C for 24 h. Soil pH and electrical conductivity (EC) were measured in a soil–water suspension (1:2.5 and 1:5 soil:water ratios, respectively) with a pH and conductivity meter (Thermo Fisher Scientific Inc., USA), respectively. The total soil organic carbon (TOC) and total nitrogen (TN) were determined via combustion of ground subsamples (passed through a 0.16 mm mesh) using an automatic elemental analyzer (Elemental Analyzer System Vario MACRO cube, Germany).

2.4. Phospholipid fatty acid analysis (PLFA)

The soil microbial community was characterized using a phospholipid fatty acids analysis as described by Bossio et al. (1998) with the slight modification by Certini et al. (2004). Lipids were extracted from 16 g of freeze-dried soil using a chloroform-methanol-citrate buffer mixture (1:2:0.8). The procedure steps are briefly described as follows: 1) extraction of lipids, 2) separation of phospholipids by solid phase extraction columns (Agilent Technologies, Inc., USA), 3) methylation of esterified fatty acids in the phospholipid fraction, and 4) GC analysis in an Agilent 6850 series Gas Chromatograph with MIDI peak identification software (version 4.5; MIDI, Inc., USA).

The following biomarkers were used: gram-positive bacteria (i14:0, i15:0, a15:0, i16:0, a16:0, i17:1 and a17:0), gram-negative bacteria (16:1 ω9c, 16:1 ω7c, i17:1 ω9c, 17:1 ω8c, 18:1 ω7c, 18:1 ω5c, cy17:0 ω7c and cy19:0 ω7c), saprophytic fungi (18:1 ω9c and 18:2 ω6c), arbuscular mycorrhizal fungi (AMF) (16:1 ω5c) and actinomycetes (16:0 10-methyl, 17:0 10-methyl and 18:0 10-methyl). The sum of the Gram-positive bacteria (G^+), Gram-negative bacteria (G^-) and non-specific bacteria (14:0, 15:0, 15:0 DMA, 16:0, 17:0, 18:0 and 20:0) was used as total bacteria (McKinley et al., 2005; Bach et al., 2010; Briar et al., 2011; Dempsey et al., 2013). All of the PLFAs indicated above were considered to be representative of the total PLFAs of the soil microbial community. The PLFA abundance was expressed in nmol g^{-1} dry soil. Fatty acids were converted into biomass carbon according to the following formulas: bacterial biomass, 363.6 nmol phospholipid fatty acid = 1 mg carbon; fungal biomass, 11.8 nmol phospholipid fatty acid = 1 mg carbon; and AMF biomass, 1.047 nmol neutral lipid fatty acid = 1 μg carbon (Olsson et al., 1995; Frostegård and Bååth, 1996; Klamer and Bååth, 2004; De Vries et al., 2013).

2.5. Soil nematode extraction and identification

Nematodes were extracted from 200 g of fresh soil by a modified cotton-wool filter method (Oostenbrink, 1960; Townshend, 1963). In each sample, the first 100 nematodes encountered on the slides were identified to genus level using an inverted microscope at 100 × magnification. Nematodes were assigned to the following trophic groups: bacterivores, fungivores, omnivores-predators, and plant parasites

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