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Relationship between home-field advantage of litter decomposition and priming of soil organic matter

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ABSTRACT

Home field advantage (HFA; acceleration of plant litter decomposition in soils that receive their indigenous litter) and priming effects (PE; short-term changes in the turnover of soil organic matter caused by the addition of fresh organic carbon) are two aspects of decomposition processes that are driven by the composition and functioning of soil decomposer communities. Physicochemical similarity between added organic compounds and soil organic matter fractions has been indicated as an important steering factor of PE. It is unknown whether PE, like litter decomposition, experience HFA, i.e., whether PE are higher than expected in soils receiving their own litter due to specialization of the decomposer community. Here we studied both HFA and PE by measuring litter- and SOM-derived carbon (C) fluxes after the addition of fresh plant litter. We reciprocally incubated three ^{13}C labelled litter types (maize, bent and beech) in soils from ecosystems where these litters are abundantly produced (e.g., arable sites, grasslands and forests), with and without the addition of mineral nitrogen (N). Generally, respiration of both litter-derived and SOM-derived C were lowest when beech litter was added, and were lower in forest soils than in arable or grassland soils. N addition generally slightly increased the respiration of litter-derived C, but had no effect on SOM-derived C. All litter types induced a positive PE in all soils. HFA effects were not significantly different from zero, but were significantly higher in grasslands than in maize fields amended with nitrogen. We found a positive relationship between litter and priming HFA, indicating that the rates of both litter decomposition and PE may be affected in the same manner by home combinations of plant and litter versus away combinations. This positive relationship disappeared when N was added. Our results provide a first indication that the extent to which indigenous soil microbes are specialized to breakdown home litter, not only accelerates or decelerates the decomposition of litter, but affects the breakdown of SOM in the same way. This could imply that a specialized litter decomposer community driving HFA can further accelerate soil C mineralization via enhanced induction of PE. Therefore, the impact of specialized decomposer communities on the dynamics of soil C pools may be bigger than expected from HFA of litter decomposition alone.

1. Introduction

Global carbon (C) cycling plays a key role in climate regulation (Crowther et al., 2016). The main source of C-CO_2 from the soil to the atmosphere is the decomposition of soil organic matter (SOM) and fresh plant litter (Schlesinger, 1997). Besides controlling carbon cycling, SOM and plant litter decomposition are crucial processes for nutrient cycling and maintaining soil fertility (Schmidt et al., 2011; Swift et al., 1979). Traditionally, the main factors assumed to control decomposition rates in different ecosystems are climatic conditions and chemical complexity of the organic material (Aerts, 1997). However, over the last decade evidence is growing that decomposer community composition may also influence decomposition processes at local scales (e.g., Bradford et al., 2017; van der Wal et al., 2015) in particular when soil (decomposer) communities differ in their capacity to decompose different substrates (Ayres et al., 2009; Keiser et al., 2011). In light of global change, it is important to understand the role of litter and SOM-degrading abilities of microbial communities in soil carbon dynamics.

Home-field advantage (HFA) and priming effects (PE) are two aspects of decomposition processes that are driven by the composition

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and functioning of soil decomposer communities. HFA is the phenomenon by which plant litter decomposition is accelerated in soils where the litter originates from (i.e., at home) compared to other soils (i.e., away) (Ayres et al., 2009; Gholz et al., 2000). This may be due to specialization of decomposer communities in the home soil compared to the away soil. PE are short-term changes, often increases, in the turnover of SOM caused by the addition of fresh organic carbon (e.g. root exudates, plant litter) to the soil (Kuzyakov et al., 2000). PE may occur when the addition of organic compounds triggers microbial production of extracellular enzymes which decompose fractions of SOM (Fontaine and Barot, 2005) or when the lack of inorganic nitrogen (N) availability in the soil stimulates microbes to mine for N in SOM (Dijkstra et al., 2013). It has been hypothesized that positive PE are stimulated when the physicochemical composition of added compounds (e.g. fresh litter) and SOM fractions are similar, because soil microbes may be specialized to decompose both added litter as well as SOM fractions (van der Wal and de Boer, 2017). This suggests, that in line with HFA for litter decomposition, PE might be accelerated in home soils (own litter and SOM combination) than in away soils, but we have no evidence for this yet.

The breakdown of plant litter and SOM is affected by the availability of nitrogen (N) in the soil (Craine et al., 2007; Knorr et al., 2005). Therefore, increased N availability may induce changes in HFA and PE. Generally, addition of N increases decomposition of high quality litters, whereas the reverse is seen for low quality litters (Knorr et al., 2005). How this affects HFA is not yet well examined, but some studies revealed that HFA effects for litter decomposition can increase with N addition (Li et al., 2017; Yu et al., 2015). The magnitude of PE may also be influenced by the availability of N (Dijkstra et al., 2013). According to the “microbial nitrogen mining” hypothesis microbes use labile C as an energy source to decompose recalcitrant organic matter and acquire N (Moorhead and Sinsabaugh, 2006). Hence, N addition may reduce mining for N and, consequently, SOM decomposition (Chen et al., 2014). However, it remains unclear how N addition changes PE in soil receiving their own or foreign litter, and therefore how HFA for litter decomposition and PE are related.

In this study we aim to understand how litter breakdown in home and away soils (litter HFA) is related to SOM decomposition in home and away soils (priming HFA). We hypothesized that (1) there is a positive relationship between litter HFA and priming HFA, i.e., in soils where litter decomposition is accelerated by the addition of home litter, PE will also be accelerated and *vice versa*, and that (2) N addition will modify the relationship between PE and HFA. To test our hypotheses we performed a microcosm experiment under controlled laboratory conditions. We incubated maize, common bent and beech ^{13}C-labelled litter in soils from arable maize fields, natural grasslands dominated by common bent and beech forests according to a full-factorial reciprocal design. We measured the amount of ^{12}C and ^{13}C respired from the microcosms, which allowed us to disentangle the decomposition rates of “older” soil organic matter (^{12}C) from “fresh” litter (^{13}C), respectively (Paterson et al., 2008). We examined litter decomposition and PE in soils receiving “home” or “away” litter, with or without the addition of mineral nitrogen.

2. Materials and methods

2.1. Soil sampling and processing

In August 2015, soil (0–10 cm, after removing the litter layer) was collected in three different types of ecosystems in the central part of the Netherlands (Table S1), i.e. arable fields, deciduous forests and natural grasslands developed on abandoned arable fields (Table 1). The arable fields were planted with maize (*Zea mays* L.), the dominant plant species in the forests was beech (*Fagus syslvatica* L.). The natural grasslands were dominated by grasses such as common bent (*Agrostis capillaris* L.), tufted grass (*Holcus lanatus* L.) and forbs such as narrow-leave plantain (*Plantago lanceolata* L.) (Table S1) (Morriën et al., 2017). For each ecosystem type, we collected soils from four separate sites that were about 1 km apart, representing four independent biological replicates for each ecosystem type (Table S1). Fresh soil was sieved (4 mm) and homogenized, removing fine roots and other plant debris, but keeping representative sized soil micro- and meso-fauna in our experimental soil incubations (Chapin et al., 2011). Field-moist soil was then stored at 4 °C until further use.

2.2. Measurement biotic and abiotic soil and litter properties

From each of our soil samples we collected a random subsample to determine biotic and abiotic soil conditions. In addition, for each of the litter types we determined C and N content.

2.2.1. Soil and litter chemical properties

Soil pH (soil: H_2O,1:2 w:v), gravimetric moisture content (dried at 105 °C, to constant mass) and maximum water holding capacity (WHC) was measured in fresh soil samples. Total C and N in all soil samples and litters were measured by a combustion method using an elemental analyser (Thermo flash EA 1112, Thermo Fisher Scientific Inc.). Mineral N was extracted by shaking 10 g dry weight soil with 50 ml 1 M KCl for two hours. Concentration of $N\text{-}NH_4^+$ and $N\text{-}NO_3^-$ in the KCl extract were determined using an AutoAnalyzer (SEAL QuAAtro Segmented Flow Analysis system). The orthophosphate fraction from the soils was extracted in a 1:20 (w/v) ratio with a 0.5 M solution of $NaHCO_3$ at pH 8.5. Concentration of $P\text{-}(PO_4)$ in the extracts was determined by an AutoAnalyzer (SEAL QuAAtro Segmented Flow Analysis system). Soil characteristics of the soils are listed in Table S1.

2.2.2. DNA extraction and quantitative PCRs

To determine bacterial biomass we extracted DNA from soils using the PowerSoil® DNA Isolation Kit (MOBIO Laboratories, Carlsbad, California, USA) according to the manufacturer's instruction with some modifications: after adding solution C1 (causing cell lysis), samples were incubated at 60 °C for 30 min; after adding solution C6 (releasing DNA from spin filter), samples were incubated at 30 °C for 10 min. Total DNA was quantified using a NanoDrop ND-1000 Spectrophotometer (Bio-Rad Laboratories Inc.).

Briefly, each qPCR reaction for bacterial quantification (total volume 15 µl) consisted of 7.5 µl of Sybergreen (iTaq™ Universal SYBR® Green Supermix), 0.6 µl of forward primer (Eub 338, 10 pmol μl^{-1}) (Amann et al. 1990), 0.6 µl of reverse primer (Eub 518, 10 pmol μl^{-1}) (Muyzer et al., 1993), 3.3 µl Nucleic acid free water (Sigma) and 3 µl of DNA. Plasmid Ter331 (Collimonas 16S) was used as a standard for the quantification. The PCR program consisted of an initial denaturation step at 95 °C for 2 min, followed by 40 cycles of 95 °C for 10 s, 53 °C for 10 s and 72 °C for 25 s. The qPCRs were performed with a Rotor-Gene RG-3000 (Corbett research). For each template DNA we analysed four biological replicates in duplicate. The results obtained, expressed as 16S rRNA gene copy numbers/g of dw soil, were used to calculate the bacterial biomass using a conversion factor of 4.1 copies per cell (Santelli et al. 2008) to estimate the bacterial cell densities and then a conversion factor of 320 fg C mm^3 to estimate the carbon content per cell (Bloem et al., 1995).

2.2.3. Fungal biomass

Ergosterol, a sterol found in fungal membranes, was used as a biomarker for fungal biomass. We used the protocol described by (de Ridder-Duine et al. 2006). Briefly, 4 g of moist soil was shaken with 6 ml of methanol in the presence of glass beads, to disrupt the fungal mycelium and to release the ergosterol into the extractant. After centrifugation and filtration, ergosterol was measured on a 1260 Bio-inert LC coupled with a 6460 QQQ (Agilent, Santa Clara, USA). The results obtained, expressed as mg kg^{-1}, were used to calculate the fungal biomass using a conversion factor of 5.4 Conversion factors of 5.4 mg