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Microbial community response to changes in substrate availability and habitat conditions in a reciprocal subsoil transfer experiment

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ABSTRACT

While habitat conditions influencing the abundance of microorganisms in topsoil are well known, these dynamics have been largely unexplored in deeper soil horizons. We investigated the effects of different substrate availabilities and environmental conditions on microbial community composition and carbon flow into specific groups of microorganisms in subsoils using a reciprocal soil transfer experiment within an acid and sandy Dystric Cambisol from a ~100-year old European beech (*Fagus sylvatica* L.) forest in Lower Saxony, Germany. Containers filled with subsoil from 10 to 20 cm (SUB20) and 110 to 120 cm (SUB120) soil depths and with additions of different amounts of ^{13}C labelled cellulose (1% and 5% of the respective organic carbon content of both soil layers) were exposed either in their home field environment or transferred reciprocally between SUB20 and SUB120 horizons for periods of one, four and twelve months. During the exposure of twelve months, ^{13}C accumulated up to 15 percent in total microbial biomass and up to 25 percent in fungal PLFAs. Similar microbial ^{13}C incorporation rates in SUB20 samples located at either 20 or 120 cm depth indicated comparable microclimatic conditions in both soil environments with no depth-dependent effects on the decomposer communities. While low nitrogen availability (when primary C-limitation was alleviated) and water content limited bacterial growth and activity at both depths, fungal abundance and activity were less affected due to their ability to efficiently exploit resources in surrounding soil by hyphal growth and higher drought resistance. Consequently, bacterial PLFAs (phospholipid fatty acids) incorporated less ^{13}C than fungi. The relatively high, from 1% to 5% cellulose addition linearly increased, ^{13}C incorporation rates in SUB120 samples at 120 cm depth clearly showed the potential of efficient carbon turnover in deeper soil layers. Spatial separation between subsoil microorganisms and their substrates may therefore be an important factor influencing carbon accumulation in subsoil.

1. Introduction

At the global scale, soil organic carbon (SOC) represents the largest active terrestrial organic carbon (C) pool, and prediction of future SOC content is a major uncertainty in climate change scenarios (Lal, 2004; Kandeler et al., 2005). Despite the much lower C concentrations in subsoil than in topsoil horizons (Jobbagy and Jackson, 2000), more than 50% of organic carbon is stored in subsoils below 30 cm soil depth (Batjes, 1996). This highlights the importance of subsoils for accurate estimates of global SOC pools and their role as sources or sinks of greenhouse gases (Harrison et al., 2011; Lal, 2004). However, there is a discrepancy between the importance of carbon pools in surface and subsurface soil horizons and the limited number of studies focusing on the key role of soil microorganisms in terrestrial C cycling (e.g. Brockett et al., 2012; Zumsteg et al., 2013).

Carbon dynamics in subsoil vary from those in topsoil; subsoils harbour relatively more stabilized soil organic matter (SOM) than topsoils, as shown by the greater radiocarbon age of SOM in subsoil horizons (Rumpel et al., 2002). A variety of mechanisms have been suggested to explain this phenomenon. For example, the enhanced stabilization of SOM is thought to be caused by spatial inaccessibility and organo-mineral interactions, separating soil microorganisms from SOM and leading to a heterogeneous distribution of stabilized C compounds (Lützow et al., 2006; Chabbi et al., 2009; Salomé et al., 2010; Dungait et al., 2012). Chemical recalcitrance, however, has been suggested as less important than stabilization of organic C by mineral interactions (Eusterhues et al., 2005).

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The lack of fresh C input as an energy source for microorganisms has been discussed as another factor which inhibits C mineralization in subsoils (Fontaine et al., 2007). The main sources of potentially available subsoil OM are root exudates and dissolved organic carbon (DOC) (e.g. Jobbagy and Jackson, 2000; Kaiser and Guggenberger, 2000). However, C availability in subsoils is highly variable, since the downward movement of these fresh C inputs occurs along preferential flow paths which are stable for long time periods (Bundt et al., 2001). Large soil volumes are therefore disconnected from the supply of fresh organic matter and result in low C turnover rates. Consequently, microorganisms in subsoil are heterogeneously distributed, with preferential colonisation in pores which are connected to preferential flow paths (Bundt et al., 2001; Nunan et al., 2003). The total microbial biomass in "hotspots" is 2–3 times higher and microbial diversity is also greater as compared to bulk soil (Marschner et al., 2012). In contrast to these microbial hotspots, microbial biomass in bulk soil generally decreases with soil depth (Taylor et al., 2002; Hartmann et al., 2009). For example, only 35% of the total microbial biomass in the first 2 m of soil depth was found below a depth of 25 cm (Fierer et al., 2003a). The decrease in microbial biomass is also accompanied by a decrease in microbial diversity and changes in community composition with increasing soil depth (LaMontagne et al., 2003; Hansel et al., 2008; Will et al., 2010). Metabolic activities of soil microorganisms in top- and subsoil also typically reflect differences in environmental conditions, while processes in subsoils are more influenced by higher sensitivity to temperature increases and nutrient availability (Fierer et al., 2003b). A study in top- and subsoils of three different forest sites in Germany concluded that enzyme activities decreased with soil depth, corresponding to declines in total C and nitrogen (N) concentrations, while the degradation of recalcitrant C compounds relatively increased with depth (Herold et al., 2014). Similarly, oxidative enzymes dominated in the bulk soil compartments of subsoils, while hydrolase activities increased in microbial hotspots such as the rhizosphere (Uksa et al., 2015). However, microbial activity in subsoil was found to be similar to that in topsoil when normalized to microbial biomass (Blume et al., 2002).

The main objective of this study was to characterize the responses of microbial decomposer communities from different subsoil horizons to altered environmental conditions and substrate availabilities. We hypothesized that (i) translocation of different subsoil samples changes local environmental conditions (DOC, nutrient inputs, oxygen availability as well as amplitudes of temperature and water availability) and consequently soil microorganisms and C turnover. Furthermore, we hypothesized that (ii) increases in substrate availability change microbial community composition and function in subsoils, with relatively greater effects as soil depth increases. We conducted a reciprocal soil transfer experiment under field conditions with subsoils from 10 to 20 and 110 to 120 cm soil depths in a ~100-year old temperate beech forest site in Lower Saxony, Germany. By adding different amounts of particulate ^{13}C-labelled cellulose we changed the quantitative substrate availability of the soil samples.

2. Materials and methods

2.1. Site description

The study site belongs to the SUBSOM-Project (www.subsom.de) and is located in the Grinderwald (52° 34′ 22″ N 9° 18′ 51″ E), a ~100-years old temperate beech (*Fagus sylvatica* L.) forest 40 km northwest of Hannover in Lower-Saxony, Germany. The climate is temperate and humid with mean annual precipitation and temperature in the time period from 1981 to 2010 of 762 mm and 9.7 °C, respectively. The climate data were provided by the German Meteorological Service (DWD) monitoring station in Nienburg in the vicinity of the study area. The soil is an acid and sandy Dystric Cambisol (IUSS Working Group WRB, 2014) with soil pH ($CaCl_2$) values ranging from 3.3 (topsoil) to 4.5 (subsoil) and mean sand, silt and clay contents of 77.3%, 18.4% and 4.4%, respectively. The mean nitrogen (N) contents were 0.45 g kg^{-1} in topsoil (10 cm depth) and 0.02 g kg^{-1} in subsoil (110 cm). Parent materials for pedogenesis are fluvial and aeolian sandy deposits from the Saale glaciation (Angst et al., 2016). Table 1 lists the soil properties of a soil profile at the Grinderwald site.

2.2. Experimental setup

In total, 12 treatments were established: soil originating from 10 to 20 and 110 to 120 cm x 3 levels of substrate availability x return of soils back into 20 and 120 cm. Each treatment was sampled in triplicate after 1, 4 and 12 months. Three beech trees with distances of between 25 and 30 m from each other and diameters at breast heights (DBH) of 35–40 cm were selected. Around each of these trees, three profile pits with a distance of 2.5 m between the tree facing profile wall and the tree were excavated. The positions of the profile pits around the trees were randomly selected. All nine profile pits had a length of 1.60 m and a depth of >1.20 m. Prior to excavation of the profile pits the litter layer was removed and stored separately. During excavation of the nine profile pits, upper subsoil from 10 to 20 cm (Bsw-Bw horizon; thereafter: SUB20) and lower subsoil from 110 to 120 cm (C horizon; thereafter: SUB120) soil depths were taken, mixed separately for the two depths and passed through a 2.0 mm sieve to remove roots and stones.

One hundred eight PVC containers (2.0 cm height, 10.5 cm inner diameter, 173.1 cm^3 volume) were filled with 242.3 g SUB20 and 277.0 g SUB120 soils, respectively. These amounts were calculated according to the soil bulk densities: 1.4 g cm^3 at 20 cm depth and 1.6 g cm^3 at 120 cm depth. The top and bottom sides were closed with micro mesh PA-material with a mesh size of 500 μm to allow vertical water flow and microbial exchange between container and surrounding soil. To manipulate quantitative substrate availability, ^{13}C enriched cellulose (1.2 atom % ^{13}C, IsoLife B.V., Netherlands) derived from maize stem (*Zea mays* L.) with a mean particle size of approximately 100 μm was added in three different concentrations to both SUB20 and SUB120 samples: no addition, 1%, and 5% of the total carbon content of the Bsw and C horizons, respectively. The amount added to the SUB20 samples was 41.2 mg ^{13}C-cellulose (1%) and 206.0 mg ^{13}C-cellulose (5%), while that to the SUB120 samples was 8.3 mg ^{13}C-cellulose (1%) and 41.5 mg ^{13}C-cellulose (5%). Cellulose and soil were thoroughly mixed to ensure homogeneous distribution of the cellulose. This resulted in six types of containers (2 soil depths x 3 cellulose additions).

The containers were incorporated into the tree-facing, undisturbed profile walls (Fig. 1). In each pit, one container of each type

Table 1
Soil parameters of the field site.

Soil horizon	Depth (cm)	pH ($CaCl_2$)	SOC (g kg^{-1})	Sand (%)	Silt (%)	Clay (%)
AE	0–2	3.3	27	70	26	4
Bsw	2–12	3.4	17	65	30	5
Bw	12–36	4.4	7	67	29	4
BwC	36–65	4.5	3	73	24	3
C	65–125	4.4	0.4	95	4	1
2C	125–150	4.1	0.1	81	11	8
2Cg	150–180	4.2	0.8	72	19	9
3C	180+	4.2	<0.1	95	4	1