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Structural evidence for soil organic matter turnover following glucose addition and microbial controls over soil carbon change at different horizons of a Mollisol

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ABSTRACT

Soil organic matter (SOM) in subsoils stores more than half of terrestrial organic carbon (C), and may sequestrate more C with increasing organic input due to its low C content (or high mineral reactivity) and high chemical stability. Organic inputs can stimulate microbial decomposition of native SOM (known as the priming effect), while being microbially decomposed and transformed into SOM. Yet, microbial controls over these processes and their influence on soil carbon change in soil profile remain elusive because of technical challenge to separate them. We overcame this challenge by employing a novel approach of combining ^{13}C and ^{12}C isotopes with quantitative solid-state ^{13}C nuclear magnetic resonance (NMR). We used soil samples taken from three soil horizons in a Mollisol profile that dominated with fused-ring aromatics for a 43-day incubation. The signal intensities of the most dominant fused-ring aromatics and nonpolar alkyl groups were reduced due to the priming effect following the addition of ^{12}C enriched glucose. Those signal intensities of O-alkyl and nonpolar alkyl groups increased in SOM spectra following the addition of ^{13}C-labeld glucose, demonstrating accumulation of glucose and microbial residues. With the increasing glucose concentration, priming effect estimated using isotopic method and the magnitudes of signal loss estimated using ^{13}C NMR both increased as exemplified for the Ap horizon soil. However, soil organic C content increased only when the added glucose concentration was beyond a previously non-quantified priming saturation threshold (between 36.0 and 100.0 g glucose-C kg^{-1} SOM-C). The increase of soil organic C was larger in the subsoils than in the topsoil due to lower microbial biomass, higher microbial growth efficiency (MGE) and mineral reactivity, which were related to the reduced priming effect and enhanced accumulation of microbial and glucose residues in the subsoils. The higher MGE in the subsoils agreed with stronger shifts of microbial community composition, characterized by phosphorous lipid fatty acid profiling, with changing glucose concentration during the incubation. Our findings highlighted the importance of priming saturation threshold, microbial mediation and mineral reactivity, but not SOM recalcitrance, in controlling the dynamics of SOM. Our study provided a novel approach to quantify these parameters and understand the controlling factors in relation to different plant types and soil types.

1. Introduction

Soil organic matter (SOM) contains more carbon (C) than plant biomass and atmospheric CO_2 combined, and more than half of soil C is stored in subsoils down to 2 m (Jobbágy and Jackson, 2000). Even minor changes of soil C may have significant implications for the

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delivery of soil functions and ecosystem services such as soil fertility and plant productivity, the global carbon cycle and climate change (Jobbágy and Jackson, 2000; Lal, 2004; Six and Jastrow, 2002). SOM derives from partial decomposition and transformation of plant, animal and microbial residues (Solomon et al., 2002) and forms intimate associations with minerals (Lehmann and Kleber, 2015). Increasing organic inputs to deep soils can be realized, e. g. through increasing root exudation and fine root biomass from deep-rooted plants as a result of elevated atmospheric CO_2 (Phillips et al., 2011). Inputs of fresh organic materials can also stimulate SOM decomposition, which is known as the priming effect (Bingeman et al., 1953; Kuzyakov et al., 2000). Soil C change depends on the trade-off between the primed SOM decomposition and transformation of inputted materials into SOM. Yet, research on these processes has been largely uncoupled, and the regulating factors on SOM turnover and soil C change remain elusive because of the technical challenges in separating these two processes (Schmidt et al., 2011; Stockmann et al., 2013).

Divergent views exist regarding the factors controlling SOM turnover and soil organic C change. Based on alkaline extraction of SOM and decomposition studies of plant-derived materials, traditional SOM concepts hold that SOM is biochemically stable due to humification of plant decomposition products (Piccolo, 2001; Stevenson, 1994) or preservation of recalcitrant compounds from plant litter (Kögel-Knabner, 2002; Sollins et al., 1996). Some studies have reported that "resistant" black C (biochar) can be decomposed (Kuzyakov et al., 2014), at an even faster rate, than other organic matter fractions (Hammes et al., 2008). Emerging concepts are then proposed that SOM is chemically diverse and physically protected through mineral association and aggregation with progressively decomposed organic products (Dungait et al., 2012; Schmidt et al., 2011). Therefore, SOM turnover and SOM stability depend less on its recalcitrance than on its accessibility to microbes (Dungait et al., 2012; Schmidt et al., 2011). However, these concepts have considered either of primed SOM decomposition and transformation of inputted organic materials, and have not been examined together (Lützow et al., 2006), or proven to be more reasonable than others (Lehmann and Kleber, 2015). In addition, the important role of soil microorganisms in regulating these processes has long been recognized (Liang and Balser, 2008; Stevenson, 1994), but only been implied in the concepts of biochemical and physical stabilization of SOM (Lützow et al., 2006; Sollins et al., 1996). Subsoils have been assumed to present a greater potential for C sequestration due to their low C content or high mineral reactivity to bind decomposition productions of inputted organic materials and due to their high SOM recalcitrance (Salomé et al., 2010; Rumpel, 2014). It is unknown whether and how different soil microbial community composition in soil profile will influence SOM turnover and soil organic C change.

The priming effects have positively related to soil microbial biomass, soil microbial community composition and substrate addition concentration (Blagodatskaya and Kuzyakov, 2008). With the use of solution state ^{1}H NMR spectroscopy, Simpson et al. (2007) have reported that microbial biomass appears to contribute > 50% of the extractable SOM fractions and ~45% of the humin fraction and accounted for > 80% of the soil nitrogen in some soils. However, direct evidence is still lacking for microbial controls over the primed SOM decomposition (Blagodatskaya and Kuzyakov, 2008; Kuzyakov et al., 2000) and formation of new SOM from microbial residues (Cotrufo et al., 2013; Kallenbach et al., 2016) following input of fresh organic materials.

Microbial growth efficiency (MGE) is defined as the proportion of added substrates used for microbial growth in comparison to microbial respiration. It affects soil microbial biomass, enzyme production and then microbial residues (Sinsabaugh et al., 2013). Some studies have shown that MGE intrinsically differs with soil type and depth when SOM is the sole C source (Spohn et al., 2016). Others have demonstrated that it changes dramatically with the quality and quantity of added substrates (Frey et al., 2013; Schneckenberger et al., 2008). The differences in MGE among soils have been ascribed to different physiological responses of distinct microbial communities (Bölscher et al., 2016; Harris et al., 2012). Mathematical models with incorporation of MGE to reflect microbial mediation over primed SOM decomposition and transformation of inputted organic materials (Cotrufo et al., 2013; Sulman et al., 2014; Wieder et al., 2013) have greatly improved the projection of global soil C storage under global warming (Wieder et al., 2013) or elevated CO_2 (Sulman et al., 2014). However, this assumption has not been experimentally confirmed. Closing this knowledge gap is critical for understanding soil C sequestration potentials among soil horizons and among soil types.

Some pioneering studies have attempted to trace structural changes of SOM after ^{13}C-enriched (^{13}C-) glucose addition by using solid-state ^{13}C nuclear magnetic resonance (NMR) spectroscopy (Baldock et al., 1989; Zhang et al., 2015). The SOM spectra in these studies include ^{13}C signals from both added ^{13}C-glucose and native SOM. As a result, native SOM decomposition cannot be structurally distinguished from new SOM formed from ^{13}C-glucose transformation. We have coupled incubation experiments using ^{13}C and ^{12}C-glucose with quantitative multiple cross polarization (multiCP) ^{13}C NMR analysis (Johnson and Schmidt-Rohr, 2014). We have taken the advantage of the fact that ^{13}C NMR detects only ^{13}C, but not ^{12}C nuclei. So structures derived from added ^{12}C-enriched (or ^{13}C-depleted) (^{12}C-) glucose are invisible to NMR. The structural differences between the ^{12}C- glucose addition and no glucose addition or ^{13}C- glucose addition can then be attributed to glucose induced SOM decomposition and transformation of glucose into SOM, respectively.

The objectives of this study are 1) to distinguish structural changes of SOM associated with glucose-induced SOM decomposition and transformation of added glucose into SOM, 2) to determine the effects of glucose addition concentration and soil horizon on the structural changes of SOM, and 3) to illustrate microbial regulation over these processes and its effect on soil C change at different soil horizons. Glucose is abundantly present in root exudates (Derrien et al., 2004) and has been used extensively as a model substrate to study the rhizosphere priming effect (Kuzyakov, 2010). Three soil samples taken from three soil horizons in a typical Mollisol profile were used because they contrasted in SOM C content, specific surface area and microbial biomass (Table 1), but contained similarly large proportion of presumably "recalcitrant" fused ring aromatic C-C (Table 2). The aromatics

Table 1
Basic soil properties in different soil horizons of the studied Mollisol profile.

Soil horizon	Soil depth (m)	pH (H_2O)	SOM-C (g kg^{-1})	TN (g kg^{-1})	C/N	$\delta^{13}C$ (‰)	SSA (m^2 g^{-1})	Soil particle size distribution (g kg^{-1})			Microbial PLFAs (mg C kg^{-1})		SMB-C (mg C kg^{-1})
								Sand	Silt	Clay	Before	After	
Ap	0–0.23	6.37	33.4	2.51	13.3	−22.9	15.6	380	248	372	15.4	20.5	551
AB	0.23–0.8	6.85	14.0	0.70	20.0	−23.6		233	352	415	4.0	4.9	335
C	> 2.0	6.50	4.9	0.39	12.7	−24.6	45.6	193	352	455	1.5	1.4	75

SOM-C, soil organic matter C; TN, total nitrogen; C/N, SOM C to TN; SSA, specific surface area; sand (> 0.02 mm), silt (0.02–0.002 mm), clay (< 0.002 mm); SMB-C, soil microbial biomass C measured using the fumigation-extraction method before incubation.