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Nutrient availability affects carbon turnover and microbial physiology differently in topsoil and subsoil under a temperate grassland

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ABSTRACT

Increasing subsoil organic carbon (C) inputs could potentially mitigate climate change by sequestering atmospheric CO_2. Yet, microbial turnover and stabilization of labile C in subsoils are regulated by complex mechanisms including the availability of nitrogen (N), phosphorous (P), and sulfur (S). The present study mimicked labile organic C input using a versatile substrate (glucose) to address the interaction between C-induced mineralization, N-P-S availability, and microbial physiology in topsoil (20 cm) and subsoil (60, 100, and 300 cm) from a temperate agricultural sandy loam soil. A factorial incubation study (42 days) showed that net losses of added C in topsoil were constant, whereas C losses in subsoils varied according to nutrient treatments. Glucose added to subsoil in combination with N was fully depleted, whereas glucose added alone or in combination with P and S was only partly depleted, and remarkably 59–92% of the added glucose was recovered after the incubation. This showed that N limitation largely controlled C turnover in the subsoil, which was also reflected by microbial processes where addition of glucose and N increased β-glucosidase activity, which was positively correlated to the maximum CO_2 production rate during incubation. The importance of N limitation was substantiated by subsoil profiles of C source utilization, where microbial metabolic diversity was mainly related to the absence or presence of added N. Overall, the results documented that labile C turnover and microbial functions in a temperate agricultural subsoil was controlled to a large extent by N availability. Effects of glucose-induced microbial activity on subsoil physical properties remained ambiguous due to apparent chemical effects of N (nitrate) on clay dispersibility.

1. Introduction

Globally, subsoils (> 0.2 m) contain more than two thirds of the soil organic carbon (SOC) within the upper 3 m soil profile (Jobbagy and Jackson, 2000). Thus, despite of low SOC concentrations in mineral subsoils, their extensive volume holds the potential for substantial carbon (C) sequestration (Jobbagy and Jackson, 2000; Rumpel, 2014). This is supported by generally slow rates of C turnover in subsoils as evidenced by high mean ^{14}C-SOC ages (Rumpel and Kögel-Knabner, 2011). The delineation of subsoils is not strictly defined, but in agroecosystems it is usually considered as the soil below the plough layer or A horizon.

Management of agroecosystems to enhance subsoil organic C storage could potentially be a strategy to mitigate climate change by reducing the increase in atmospheric CO_2 concentration (Lorenz and Lal, 2005; Kell, 2011; Lynch and Wojciechowski, 2015). Principally, organic C sequestration in subsoils is controlled by the balance between organic matter inputs and losses. Inputs occur predominantly in the form of plant litter, rhizodeposition (including root exudates), and dissolved organic C, whereas losses mainly result from microbial respiration, which is linked to microbial population dynamics and activity (Fernandes et al., 1997; Hedges et al., 2000; Michalzik et al., 2003; Wilhelm et al., 2004). Hence, organic C inputs, e.g., by deep rooted crops, are required for increasing the subsoil C content, but the eventual long-term C sequestration depends on the interaction between C input and microbial activity, also involving physico-chemical mechanisms of C stabilization (Salomé et al., 2010; von Lutzow et al., 2006). It is generally acknowledged that three major mechanisms control the persistence of organic C in soils, i.e., (i) selective preservation through chemical recalcitrance of organic substrates, (ii) physico-chemical stabilization through interaction between organic C and soil minerals, and (iii) spatial separation of organic C from decomposition by microbes and extracellular enzymes (Krull et al., 2003; Lorenz and Lal, 2005; Schmidt et al., 2011). In nutrient poor subsoils, microbial mineralization of deposited organic C could also be limited by stoichiometric constraints in the availability of nitrogen (N), phosphorous (P) and/or

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Table 1
Soil chemical, physical and biological properties. OC, organic carbon; TN, total nitrogen; TP, total phosphorus; TS, total sulfur; β-Glu, β-glucosidase activity; NP, nitrophenol, PLFA, phospholipid fatty acids. Particle size distribution are shown as clay (< 2 μm), silt (2–63 μm), and sand (63–2000 μm). Data were adapted from Z. Liang et al. (unpublished data).

Depth (cm)	Horizon	OC (mg/g)	TN (mg/g)	TP (mg/g)	TS (mg/g)	Olsen-P (μg/g)	K (μg/g)	pH ($CaCl_2$)	Clay (%)	Silt (%)	Sand (%)	Density (g/cm^3)	β-Glu (μg NP/g/h)	PLFA (nmol/g)
20	Ap	21.4	1.60	1.05	0.21	39	40	5.4	7.7	29.9	58.6	1.4	9.2	16.4
60	Bw1	1.8	0.13	0.19	< 0.04	7	36	4.9	9.6	26.0	64.0	1.7	0.4	1.9
100	Bw2	0.9	0.10	0.15	< 0.04	6	54	4.2	13.1	23.2	63.6	1.8	nd[a]	1.2
300	C	0.4	0.03	0.29	< 0.04	12	54	5.1	12.0	25.5	62.4	1.7	nd[a]	0.2

[a] nd, not detectable.

sulfur (S) as related to the requirements in microbial biomass, where C:N:P:S typically occur at a ratio of around 100:15:2:1 (Xu et al., 2013, 2015). As shown in studies of Australian soils, sequestration of stable organic C in subsoils may eventually depend on products of microbial anabolism, which are enhanced by balanced stoichiometry of C:N:P:S according to microbial biomass requirements (Orgill et al., 2017). Yet, a recent study of acidic tropical forest and plantation soil concluded that the role of subsoil as a long-term sink of SOC could be questioned under conditions of increased N and P availability due to alleviation of microbial nutrient limitation (Meyer et al., 2018). Such apparently divergent results may be reconciled through the interaction of mechanisms related to microbial physiology, C turnover and C stabilization, but so far these interactions are poorly studied in subsoils. In particular, microbial dynamics related to subsoil C sequestration may depend on abiotic and biotic soil properties, including nutrient availability, which need to be better understood.

In the present laboratory study, we mimicked labile organic C input to a temperate agricultural sandy loam soil down to 300 cm depth using a simple, versatile substrate (glucose), which can be mineralized by the majority of heterotrophic microorganisms (Baldock and Oades, 1989; Hill et al., 2008). We tested the role of N, P and S availability on C mineralization, microbial physiology, and soil structural stability (clay dispersibility). The aim was to pursue whether different nutrient availability would link to an effect on microbial metabolism and soil properties, which could lead to divergent subsoil development and resultant conditions for C sequestration.

2. Materials and methods

2.1. Soil sampling and characterization

Soil was sampled in December 2015 from an excavated soil profile (0–300 cm) under an unfertilized temperate grass field at Foulumgaard Experimental Station, Aarhus University, Denmark (56°29′N, 9°34′E). The soil was a sandy loam, classified as Typic Hapludult, with an upper black Ap horizon (0–40 cm) overlaying a slightly weathered Bw_1 horizon (40–70 cm) and a Bw_2 horizon showing signs of clay accumulation (70–100 cm). The lower part of the soil profile was a rather uniform clayey C horizon (100–300 cm). The B and C horizons were light brown without visual signs of redox interphases related to anoxic conditions (such as pseudogleys). Fragments of roots were seen in the Ap and Bw_1 horizons. Soils were sampled at 20, 60, 100 and 300 cm depth from three sides of the excavated profile walls and pooled to cover small-scale heterogeneity. The soils were air dried, sieved (< 2 mm), and stored at 2 °C until use. Chemical, physical and biological properties of the soil horizons are shown in Table 1.

2.2. Carbon turnover at different C:N:P:S stoichiometry

Carbon turnover to CO_2 was measured in an automated set-up with 50-g soil samples (dry wt basis) incubated at 40% water holding capacity (WHC) by adding appropriate volumes of water or nutrient solutions. Seven treatments were prepared with different ratios of added C, N, P, and S from autoclaved solutions of glucose (2.5 mg glucose C g^{-1} soil), KNO_3, KH_2PO_4, and K_2SO_4 in demineralized (dem) water. The seven treatments represented amendments with (i) dem water as reference (Ref), (ii) glucose (Glu), (iii) glucose plus P and S at a C:P:S ratio of 100:1:1 (Glu + PS), (iv) glucose plus N at a C:N ratio of 10 (Glu + CN10), and glucose plus N, P and S at three different C:N:P:S ratios of (v) 100:10:1:1 (Glu + PS + CN10), (vi) 100:5:1:1 (Glu + PS + CN20), and (vii) 100:1.67:1:1 (Glu + PS + CN60). Nutrient solutions were mixed in appropriate stoichiometry for each treatment, pH was adjusted to native soil pH (Table 1), and after autoclaving (121 °C, 30 min) the solutions were added dropwise to soil conditioned in 100-cm^3 steel rings. Three treatment replicates were prepared for each soil horizon (i.e., 84 soil