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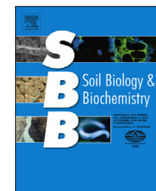

Biochemistry of hexose and pentose transformations in soil analyzed by position-specific labeling and ^{13}C-PLFA

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ABSTRACT

Microbial transformations are key processes of soil organic matter (SOM) formation, stabilization and decomposition. Combination of position-specific ^{13}C labeling with compound-specific ^{13}C-PLFA analysis is a novel tool to trace metabolic pathways. This combination was used to analyze short-term transformations (3 and 10 days after tracer application) of two key monosaccharides: glucose and ribose in soil under field conditions. Transformations of sugars were quantified by the incorporation of ^{13}C from individual molecule positions in bulk soil, microbial biomass (by CFE) and in cell membranes of microbial groups classified by ^{13}C-PLFA.

The ^{13}C incorporation in the Gram negative bacteria was higher by one order of magnitude compared to all other microbial groups. All of the ^{13}C recovered in soil on day 3 was allocated in microbial biomass. On day 10 however, a part of the ^{13}C was recovered in non-extractable microbial cell components or microbial excretions. As sugars are not absorbed by mineral particles due to a lack of charged functional groups, their quick mineralization from soil solution is generally expected. However, microorganisms transformed sugars to metabolites with a slower turnover. The ^{13}C incorporation from the individual glucose positions into soil and microbial biomass showed that the two main glucose utilizing pathways in organisms – glycolysis and the pentose phosphate pathway – exist in soils in parallel. However, the pattern of ^{13}C incorporation from individual glucose positions into PLFAs showed intensive recycling of the added ^{13}C via gluconeogenesis and a mixing of both glucose utilizing pathways. The pattern of position-specific incorporation of ribose C also shows initial utilization in the pentose phosphate pathway but is overprinted on day 10, again due to intensive recycling and mixing. This shows that glucose and ribose – as ubiquitous substrates – are used in various metabolic pathways and their C is intensively recycled in microbial biomass.

Analyzing the fate of individual C atoms by position-specific labeling deeply improves our understanding of the pathways of microbial utilization of sugars (and other compounds) by microbial groups and so, of soil C fluxes.

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1. Introduction

Soil organic carbon (SOC) plays a major role within the global C cycle as soils can function as a source or sink of atmospheric C. Plant residues and rhizodeposits are the main sources of organic matter in soils (Rasse et al., 2005). Therefore, many studies have focused on decomposition, microbial utilization and stabilization processes of C from these sources in soils.

The low molecular weight organic substances (LMWOS) play a crucial role within the C cycle in soil. Although their portion of SOC is quite low, they represent the SOC pool with the highest turnover (1–10 h mean residence time) and a quantitatively relevant gross flux of C passes through this pool (30% of total CO_2 efflux) (van Hees et al., 2005). LMWOS are defined as the lightest components of dissolved organic carbon (DOC) with a molecular weight lower than 250 Da (Boddy et al., 2007). Their main sources are exoenzymatic depolymerization of above- and belowground litter as well as rhizodeposition. Microorganisms determine the fate of LMWOS in

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soil because they are able to either produce them, decompose them to CO_2 (catabolism) or incorporate them in cellular compounds (anabolism). Microbial incorporation and transformation of LMWOS are key processes in stabilizing soil organic carbon (SOC) (Miltner et al., 2012; Simpson et al., 2007). Therefore, microbial transformation pathways of LMWOS represent a crucial step of soil C and N fluxes, and a molecular-level knowledge of these processes is needed (van Hees et al., 2005).

Besides amino acids and carboxylic acids, sugars are a main component of LMWOS (van Hees et al., 2005). Sorption and other interactions with soil organic matter (SOM) are nearly irrelevant for sugars, as they have neither charged functional groups nor hydrophobic molecule parts. Thus, their fate is mainly determined by microbial utilization. They can occur as monosaccharides with a five C backbone (pentoses) or a six C backbone (hexoses) or as di- or oligosaccharides within the LMWOS. Individual monosaccharide concentrations in soil solutions typically range from 1 to 10 μM (Fischer et al., 2007). Within this class, glucose is most abundant monomer, deriving from the decomposition of plant residues as well as rhizodeposition (Kuzyakov, 2010), and is known to be a ubiquitous substrate for microorganisms (Macura and Kubatova, 1973). The main sources of pentoses in soil are plant hemicelluloses (Cheshire et al., 1971; Koegel-Knabner, 2002), but ribose in particular is actively formed in soils (Murayama, 1988), e.g. for the biosynthesis of ribonucleotides and their polymers (DNA and RNA).

Sugar monomers are the building blocks of different polysaccharides (e.g. cellulose, starch), and are also precursors of the ribonucleotide backbone and cell wall polymers. Microorganisms can degrade all of these polymers to monosaccharides or *vice versa*, build them up from monosaccharides. However, sugars are not only anabolic substrates but also a preferred source for energy production in catabolism. For glucose, it was known that an average of 60% is incorporated in cellular compounds and 40% is oxidized to gain energy (Fischer et al., 2010), but there is no information whether this ratio is similar for other monosaccharides. This ratio can be influenced by many factors like the nutritional state of microorganisms or the supply by further LMWOS. In addition, individual functional groups of the microbial community are expected to use LMWOS-C in different pathways and produce various metabolites from them. To date, neither the metabolic pathways of monosaccharides nor the specifics of individual functional groups of the soil microbial community are investigated in soils. The combination of position-specific labeling with compound-specific isotope analysis is a unique approach, which enables tracing the transformations of LMWOS within the microbial community of soils (Apostel et al., 2013). Position-specific labeling – a tool that is commonly used in biochemistry to investigate metabolic pathways – has recently reached an increasing consideration in soil science (Fischer and Kuzyakov, 2010; Dijkstra et al., 2011a; Apostel et al., 2013; Dippold and Kuzyakov, 2013). It overcomes the limitations of uniform labeling because it allows differentiation between the incorporation of molecule fragments vs. the incorporation of entire intact molecules and thus enables the reconstruction of metabolic pathways. PLFA analysis not only allows a reconstruction of the microbial community composition (Zelles et al., 1995; Zelles, 1999), but in combination with ^{13}C labeling – i.e. ^{13}C-PLFA analysis - also enables tracing of substrate incorporation and reconstruction of sugar metabolism of individual microbial groups (Glaser, 2005).

This study aimed to trace C transformations of monosaccharides in soil. The hexose glucose and the pentose ribose were applied position-specific ^{13}C labeled to undisturbed soil cores and the ^{13}C incorporation in microbial biomass and PLFA was traced over 10 days. As sugars possess no functional groups with which they could interact with the soil matrix, we hypothesize complete uptake into the microbial biomass. In addition, we state the hypothesis that the incorporation of glucose into microbial biomass and bulk soil reflects the oxidation pattern of glycolysis i.e. preferential oxidation of C-3 and C-4 positions to CO_2. In contrast, the pentose phosphate pathway may dominantly affect ribose utilization and lead to a preferential loss of ribose C-3, C-1 and C-2 as CO_2. If glucose is utilized in this pentose phosphate pathway, we will detect a loss of the glucose C-1and C-4 positions. Furthermore, we hypothesize that pathways of eukaryotes and prokaryotes differ, which will be reflected in the different incorporation of glucose and ribose C positions into the specific PLFAs of these microbial groups.

2. Materials and methods

2.1. Field experiment

2.1.1. Sampling site

The field experiment is located on an agriculturally used loamy Luvisol in northern Bavaria (49°54′ northern latitude; 11°08′ eastern longitude, 500 a.s.l.) with a mean annual temperature of 7 °C, and a mean annual precipitation of 874 mm. The last crop was *Triticale*. The soil had a pH_{KCl} of 4.88, a pH_{H2O} of 6.49, a TOC and TN content of 1.77% and 0.19%, respectively. CEC was 13 $cmol_C\ kg^{-1}$.

2.1.2. Experiment design

Field experiment is described in detail in Apostel et al. (2013). Briefly, the 12 × 12 m field was divided into four quadrants, for four replications. PVC-tubes (diameter: 10 cm, height: 13 cm) were installed 10 cm deep in the soil. 10 ml tracer-solution per column were applied with a multipette (Eppendorf, Hamburg, Germany) with concentrations of ^{13}C-labeled sugars according to Table 1. A 7 cm long needle with lateral holes enabled homogeneous distribution of the tracer solution within the column. The solution was only injected in the upper 2/3 of the column to avoid leaching and rainfall was blocked by a roof. In each of the quadrants and for both sampling times, glucose and ribose were applied once as 1) nonlabeled background, 2) uniformly ^{13}C-labeled, and 3) as four and two position-specific ^{13}C-labeled isotopomeres of glucose and ribose, respectively (see Table 1) with a random distribution within the block.

2.1.3. Sampling and sample preparation

Sampling occurred 3 and 10 days after labeling. Complete columns from one set (background, uniformly and position-specifically labeled) were dug out. Soil volume and density were determined; a subset was sieved to 2 mm for further analysis and

Table 1
Locations of ^{13}C in position-specific labeled glucose and ribose and their amounts added to soil in the field experiment.

	Glucose					Ribose		
	^{13}C-1	^{13}C-2	^{13}C-4	^{13}C-6	U-^{13}C	^{13}C-1	^{13}C-5	U-^{13}C
C concentration (μmol ml^{-1})	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.09
C amount (μmol g $soil^{-1}$)	2.72	2.77	2.76	2.73	2.93	2.70	2.70	2.71
Atom% ^{13}C	12.36	12.36	12.43	12.34	12.71	12.83	12.82	13.46

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