



Aggregate size and glucose level affect priming sources: A three-source-partitioning study



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ABSTRACT

Decomposition of soil organic matter (SOM) protected within aggregates can be accelerated via priming effect (PE) by the addition of fresh substrates. However, the knowledge of the sources of mineralization and PE in aggregate size classes is absent. We applied the three-source-partitioning isotopic (¹⁴C + δ¹³C) approach to determine how aggregate size classes affect the contribution of three C sources (substrate added, recent and old SOM) to CO₂ efflux and PE depending on the amount of added primer. Soil from a field with 3 years of maize cropping (C₄ plants) after long-term C₃ vegetation was used to differentiate between recent C (C₄-C; < 3 years) and old C (C₃-C; > 3 years). Soil samples were separated into three aggregate size classes (>2 mm, 2–0.25 mm macroaggregates and <0.25 mm microaggregates) and were incubated for 49 days after being amended with two levels of ¹⁴C labeled glucose.

The proportion of glucose mineralized to CO₂ increased with decreasing aggregate size, but ¹⁴C incorporation into microbial biomass decreased, indicating higher C use efficiency in macroaggregates compared with microaggregates. The short-time PE was positive and was accompanied by a rapid reduction of dissolved organic C. After 49 days, the PE was higher in macro-versus microaggregates at both glucose levels. Positive PE induced by a low glucose level was observed only in large macroaggregates (>2 mm), but was observed in both macroaggregates (>0.25 mm) and microaggregates (<0.25 mm) after high glucose amendment. These results indicate that SOM pools are more decomposable in macro-versus microaggregates and that the SOM pools are involved in PE according to their biochemical availability. More primed CO₂ originated from recent C₄-C than old C₃-C in larger macroaggregates under a low glucose level. The relative contribution of recent C₄-C to primed CO₂ increased from macroaggregates (37.8%) to microaggregates (100%) after high glucose amendment. Therefore, increasing glucose addition stimulated the decomposition of old C₃-C in macroaggregates, but not in microaggregates. This indicates that microaggregates protect SOM against decomposition better than macroaggregates, and consequently, microaggregates can be considered as a potential reservoir for long-term C sequestration.

Concluding, aggregate size is crucial for SOM decomposition, and it determines the source of PE and thus the protection of sequestered C. The effects of the added primer on C sources involved in PE depend on the aggregate size.

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1. Introduction

The input of readily available substrates to the soil can alter carbon (C) sequestration by modifying the mineralization of the native soil organic matter (SOM) pool via priming effect (PE) (Kuzyakov, 2010). The SOM is not chemically uniform and consists

of various pools with varying levels of degradability and turnover rates (Stevenson, 1994; Von Lützwow et al., 2007). Therefore, it is important to consider the contribution of individual SOM pools to CO₂ release and to investigate the extent to which various pools are involved in PE.

Soil organic matter occlusion within aggregates is one of the most important physical preservation mechanisms because there are physical barriers between microorganisms, enzymes and their substrates (Six et al., 2002). Using the “aggregate hierarchy” hypothesis, it is generally accepted that microaggregates (<0.25 mm) can afford the most protection to associated SOM. This is because the SOM associated with microaggregates is formed by primary particles coupled together by plant and microbial debris and by humic materials or polysaccharide polymers, which better protect SOM against decomposition than macroaggregates (>0.25 mm) (Elliott, 1986; Six et al., 2002; Deneff et al., 2007; Kimura et al., 2012). Additionally, SOM preferentially stabilized in microaggregates can be better protected against decomposition within stable macroaggregates (Six et al., 2000; Six and Paustian, 2013). Turnover of SOM is assumed to be more rapid in macroaggregates than in microaggregates (Besnard et al., 1996; Six et al., 2002; Gunina and Kuzyakov, 2014). This assumption was confirmed with more SOM mineralized from macroaggregates (>0.25 mm) versus microaggregates (<0.25 mm) (Gregorich et al., 1989; Mutuo et al., 2006), with higher PE also observed in macroaggregates (>0.25 mm) compared with microaggregates (<0.25 mm) (Tian et al., 2015). However, there is no consensus on the effects of aggregate size classes on SOM decomposition because the greatest CO₂ production is from the microaggregates (Seech and Beauchamp, 1988; Drury et al., 2004; Sey et al., 2008), and no differences between macro- and microaggregates have been reported (Rabbi et al., 2014). Furthermore, an increase in PE intensity with decreasing particle size has been observed, which has shown not only that the labile pools in aggregates are affected but also that more stable pools are characterized by higher ¹⁴C ages (Ohm et al., 2007; Negassa et al., 2015).

To identify the SOM pools responsible for mineralization and PE, more than two C sources should be labeled (Kuzyakov, 2010). Despite recent progress in the partitioning of three C sources (added substrate, recent and old C) in SOM (Kuzyakov and Bol, 2006; Fontaine et al., 2007; Blagodatskaya et al., 2011, 2014; Derrien et al., 2014), there is still a lack of information on such partitioning within aggregate size classes.

Generally, a positive correlation between the amount of an added labile substance and its microbial mineralization has been observed (Bremer and van Kessel, 1990; Mary et al., 1993; Schneckenberger et al., 2008). In addition, it has been shown that the priming of SOM decomposition increased with the increased addition of labile substrates until saturation of the microbial utilization capacity (Blagodatskaya and Kuzyakov, 2008; Paterson and Sim, 2013). However, it is not only the labile pools of SOM that are easily affected by PE, but also the SOM pools with low degradability (Hamer and Marschner, 2005). The SOC fractions with low degradability can be affected by PE after repeated substrate inputs (Fontaine et al., 2007; Mau et al., 2015) and high amounts of primer (Blagodatskaya et al., 2011). In addition to the recalcitrance of SOM pools, all these studies have suggested that the availability of the primer is a limitation for the degrading microorganisms and that this is a major factor controlling the extent of SOM decomposition.

We hypothesized that (1) more C would be mineralized and a higher PE would be observed in macroaggregates because SOM is less recalcitrant and more easily decomposable than in microaggregates (Elliott, 1986; Six et al., 2002; Deneff et al., 2007) and, consequently, the SOM pools involved in PE vary according to their

biochemical availability (Blagodatskaya et al., 2011); (2) compared with macroaggregates, the PE in microaggregates would require higher levels of primer addition; (3) the relative contribution of recent C sources to the PE would be greater in macro-versus microaggregates. This hypothesis is because macroaggregates have more easily decomposable C (e.g., recent C) (Elliott, 1986; Six et al., 2002; Deneff et al., 2007) and microorganisms will preferentially utilize labile substrate (Paterson et al., 2007; Kuzyakov, 2010), but the extent may depend on the primer amount. To test these hypotheses, we combined the recently developed isotopic approach for three-C-source-partitioning (substrate added, recent and old SOM) with fractionation of aggregate size classes and measured three fluxes and pools: CO₂, microbial biomass C (MBC) and dissolved organic C (DOC).

2. Materials and methods

2.1. Soil sampling and aggregate preparation

Soil (loamy Haplic Luvisol originated from loess) was sampled in April 2012 from the upper layer (0–10 cm) of a maize field as well as from an adjacent wheat field located northwest of Göttingen, Germany. The soil had 5.8% sand, 87.2% silt and 7.0% clay according to the German classification system. The C₄ plant maize (*Zea mays*) was grown for three years after long-term C₃ cropping with wheat (*Triticum aestivum*). The experimental design was described in detail by Kramer et al. (2012) and Pausch and Kuzyakov (2012).

The soil samples were transported to the laboratory, where plant roots and leaves were carefully removed by hand picking, and the soil samples were then stored at 4 °C for no longer than one week before aggregate processing. The soil was sieved to separate large macroaggregates (>2 mm), small macroaggregates (2–0.25 mm) and microaggregates (<0.25 mm) according to Tian et al. (2015). Soil was first gently manually crumbled to approximately 5 mm pieces, transferred to two sieves (2 and 0.25 mm), and shaken for 2 min. Thereafter, the aggregates remaining on top of the sieves were collected. Large macroaggregates were collected from the 2 mm sieve, small macroaggregates from the 0.25 mm sieve, and microaggregates that passed through the 0.25 mm sieve. The soil aggregates were then spread out in a thin layer and air-dried. Preliminary tests showed that the sieving duration was sufficient to separate the various aggregates size classes while minimizing aggregate abrasion during the sieving process (Dorodnikov et al., 2009).

The vegetation change from C₃ to C₄ crops caused a shift in the δ¹³C values of soil and of the aggregates (Table 1). Hence, through the vegetation change from C₃ to C₄ crops, a distinct isotopic signal was introduced into the soil that allowed for partitioning of old SOM (C₃-C) and recent SOM (C₄-C). Hereafter, C₄-derived C is referred to as “recent” C (<3 years), and C₃-derived C, which entered the soil before maize cropping, is referred to as “old” C (>3 years).

Table 1
SOC and δ¹³C content in aggregate size classes in the reference and maize soils.

Soil type	Aggregate size classes	SOC (g kg ⁻¹)	TN (g kg ⁻¹)	δ ¹³ C[‰]
C ₃ reference soil	>2 mm	13.0	1.29	-26.45
	2–0.25 mm	13.6	1.39	-26.51
	<0.25 mm	12.4	1.27	-26.34
C ₃ -C ₄ soil	>2 mm	12.3	1.26	-23.81
	2–0.25 mm	13.7	1.30	-23.87
	<0.25 mm	11.5	1.20	-23.20

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