Is the fate of glucose-derived carbon more strongly driven by nutrient availability, soil texture, or microbial biomass size?

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ABSTRACT

Increasing organic matter (OM) in soil promotes the delivery of vital ecosystem services, such as improving water retention, decreasing erosion, increasing plant productivity, and mitigating climate change through terrestrial carbon (C) sequestration. The formation of organo-mineral associations through microbial turnover of labile (i.e. easily decomposed) C is a potential pathway of soil C stabilization. However, association of added C with mineral surfaces may be impacted by soil clay content and/or by nutrient availability (due to higher microbial C use efficiency). We added ^{14}C labeled glucose as a model labile substrate together with either ion exchange resin beads (to induce nutrient limitation), water (no additional nutrients), or four increasing concentrations of nitrogen, phosphorus, and sulfur in constant stoichiometric ratios to nine agricultural soils under the same climate and management but along a texture gradient from 3 to 40% clay. The soils with ^{14}C-glucose and a nutrient treatment were incubated for 4 weeks during which the ^{14}C was traced into CO_2, microbial biomass, dissolved organic C (DOC), and soil organic C (SOC). Induced nutrient limitation (available C:N ratio around 300:1) reduced mineralization of glucose-derived C, particularly in soils with <15% clay. However, in soils with ≥15% clay, higher microbial biomass allowed for glucose-derived C mineralization despite nutrient limitation. Alleviating the nutrient limitation (available C:N < 50:1) allowed for greater transformation of added C into microbial biomass-C and SOC, particularly in soils with ≥21% clay, although further additions (down to C:N of 11:1) did not result in greater SOC or microbial biomass formation. Except under conditions of nutrient limitation (where C:N > 50:1), soil texture and starting microbial biomass size, not nutrient availability, were the drivers of SOC and microbial biomass formation during the incubation.

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1. Introduction

The use of fertilizers containing (N), phosphorus (P), and sulfur (S) to increase food production has made humans a dominant driver of global nutrient cycling, which will likely continue as we seek to sustainably intensify agricultural productivity (Vitousek et al., 1997; Foley et al., 2011). As the cycling of nutrients in soils is inextricably linked to the turnover of soil organic carbon (C), adding nutrient fertilizers to soil may alter soil C cycling (Gärdenäs et al., 2011). Soil organic matter (SOM) is a large global pool of C

(>1500 Pg C to depths of 1 m or more) that if mineralized can act as a C source, or if accumulated can act as a C sink, potentially offsetting anthropogenic greenhouse gas emissions (Lal, 2004). As a result, a thorough understanding of the impact of nutrient availability on soil C turnover is required to predict its potential response to increases in inorganic fertilization.

Carbon is stabilized in soil by a variety of mechanisms. Historically the chemical composition of SOM was thought to dictate its turnover, with greater stabilization of more complex biopolymers due to slower rates of decomposition (Derenne and Largeau, 2001). However, recent work emphasizes that microbial access to SOM, rather than chemical composition, controls its turnover (Dungait et al., 2012). Microbial access to SOM is restricted by C association with mineral surfaces and by spatial isolation within soil aggregates (Jastrow et al., 2007). The importance of mineral surfaces for SOM

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stabilization has been recognized for decades, with increases in reactive mineral phases corresponding to increases in the potential for carbon accumulation (Hassink, 1997; Baldock and Skjemstad, 2000; Six et al., 2002).

Although OM sorption and co-precipitation play an important role in C protection on mineral surfaces (Kramer et al., 2010; Kleber et al., 2015), microorganisms, as the "eye of the needle" through which SOM is processed (Jenkinson, 1978), are increasingly recognized as dominant drivers of SOM formation and longer-term stabilization. Improved analytical techniques have established that mineral-bound OM is predominately derived from microbial products (Miltner et al., 2011), with a layering of OM on clay particles where proteins and polysaccharides from microbial residues aid in additional mineral-OM stabilization (Kleber et al., 2007). Therefore, organo-mineral associations can be formed during OM decomposition as microbial residues associate with mineral surfaces (Cotrufo et al., 2013). The quantity of microbial-derived organic matter (MOM) formed through this pathway is dependent on the amount of MOM produced during decomposition as well as the capacity of mineral surfaces to protect MOM from further decomposition (Six et al., 2006).

The quantity of MOM formed during decomposition depends on whether decomposing OM is initially released as CO_2 or used to build microbial biomass, also known as microbial carbon use efficiency (CUE) or microbial growth efficiency (MGE). There is increasing recognition that changes in CUE due to C substrate quality, elevated temperatures, or changes in microbial community composition can alter C stocks in response to climate change (Allison et al., 2010; Frey et al., 2013; Wieder et al., 2014). Therefore, modification of these CUE drivers may result in enhanced soil C accumulation, even with lower C inputs (Kallenbach et al., 2015). Interesting, the chemical complexity of C inputs appears to dictate the pathway of soil C formation through this CUE control, with labile C inputs (i.e. easily degradable C, metabolic plant components) forming greater quantities of mineral-bound C (i.e. protected) than chemically complex inputs (i.e. structural plant components), potentially due to higher CUE (i.e. greater allocation of substrate-C to microbial biomass-C than to CO_2; Bradford et al., 2013; Cotrufo et al., 2015; Haddix et al., 2016).

In addition to substrate quality, nutrient addition can impact OM formation, with higher CUE as nutrient availability increases (Schimel and Weintraub, 2003; Hessen et al., 2004). The increase in CUE with nutrient availability is based upon the concept of nutrient stoichiometry, where microbial biomass has a constrained C:N:P:S ratio (Cleveland and Liptzin, 2007; Kirkby et al., 2011), and so theoretically more microbial biomass is formed (and less C respired) as the available C: nutrient ratios approach the ratios required for optimum growth (around 20–25:1 for C:N in terrestrial microorganisms; Manzoni et al., 2012; Sinsabaugh et al., 2013). Operating under this mechanism, (due to high microbial contributions to mineral-associated OM) increases in nutrient availability should increase stabilization of C in the finer textured fractions of soil (Neff et al., 2002; Cenini et al., 2015). However, the influence of C complexity and nutrient availability on CUE could be confounded by other potential drivers, such as changes in microbial community structure and function. For example, N deposition can decrease the abundance of C-use efficient oligotrophic bacteria and fungi (Leff et al., 2015) or cause microorganisms to adjust their nutrient use efficiency (Mooshammer et al., 2014), thereby impacting microbial biomass formation. The timescale over which CUE is measured is also of critical importance: over longer timescales (e.g. weeks) this ecosystem-level CUE includes the turnover of microbes and microbial residues (Geyer et al., 2016), which may respond more strongly to climate and nutrient availability (Hagerty et al., 2014; Kaiser et al., 2014) than shorter-term changes that exclude

microbial turnover. Importantly, whether microbial residues formed from added C remain in soil depends on whether that biomass is protected from further decomposition, likely due to association with mineral surfaces (Throckmorton et al., 2014).

In this context, the purpose of our experiment was to determine whether nutrient availability or edaphic properties (specifically clay content and microbial biomass size) influenced the fate of an added labile C substrate along a natural field-based gradient in soil texture (3 to 40% clay). In our experiment, we define labile C as dissolved substrates that can be rapidly assimilated by a large portion of the microbial community, and we use glucose as a model compound. We define stabilized soil C as that which is not mineralized to CO_2 and therefore remains in the soil, with the recognition that this definition is dependent upon the timescale of measurement (which for this experiment is four weeks). The concept was to (1) add a readily utilized, soluble, and ^{14}C labeled substrate with limited abiotic sorption potential (glucose) as a tracer at concentrations high enough to increase microbial biomass, (2) determine whether nutrient additions changed the allocation of substrate C to biomass versus CO_2 over four weeks, and then (3) assess whether clay content impacted the quantity of glucose-derived C remaining in the soil as microbial biomass and soil C. We hypothesized that soils with higher clay contents would have a greater capacity to protect formed glucose-derived SOC and microbial biomass from further decomposition, thereby decreasing mineralization of glucose-derived C as CO_2 (independent of nutrient addition). We also hypothesized that higher nutrient availability would lead to greater formation of microbial biomass, and that the quantity of MOM remaining in the soils after four weeks would increase with clay content.

2. Materials and methods

2.1. Soil sampling and site description

Soil samples were taken within a 1-m radius of previously identified points (Murphy et al., 2009) from a field with a naturally occurring clay gradient near Dangin in Western Australia (32°5′S, 117°18′E). The region has a semi-arid climate, with hot, dry summers and cool, wet winters (when cropping occurs). Based on 15 years of climate data (1997–2014) the area has a mean annual rainfall of 326.5 mm, and mean annual temperature of 25.4 °C. Soils from nine sites across a texture gradient ranging from 3 to 40% clay were sampled when the soil was in a dry state (Austral autumn 2014 prior to seeding) within a 10 ha area of the field. After removing plant residues and surface debris, five soil cores of the surface 0–10 cm layer (Ap horizon) were taken at each site using a 10 cm diameter push-in auger and composited. After sampling, soils were stored at 4 °C, air-dried at 40 °C, sieved to <4 mm, and then characterized and incubated as described below.

At one of the sampling sites (21% clay), 2.5 t ha^{-1} of gypsum was applied in 2008, but otherwise management was consistent across the sites. Inorganic N application rates in this region to winter wheat typically vary from 0 to 100 kg N ha^{-1}, based upon expected yields (average yields of 1.9 t ha^{-1} for winter wheat) and anticipated growing season rainfall (200–400 mm). Nitrogen fertilization contributes about 20% of total N to wheat cropping systems in Australia, so that these low input farming systems are highly reliant on biological N fixation and SOM mineralization to meet crop N demands (Angus, 2001). As a result, microbial turnover of SOM is an important nutrient supply for plants in this system.

2.2. Soil characterization

Percentage distributions of sand (20–2000 μm), silt (2–20 μm),