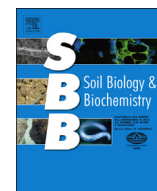




Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Microbial physiology and necromass regulate agricultural soil carbon accumulation

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ARTICLE INFO

Article history:

Received 3 May 2015

Received in revised form

5 September 2015

Accepted 10 September 2015

Available online xxx

Keywords:

Soil carbon

Microbial carbon use efficiency, CUE

Growth rate

Organic agriculture

Cover crops

ABSTRACT

Strategies for mitigating soil carbon (SOC) losses in intensively managed agricultural systems typically draw from traditional concepts of soil organic matter formation, and thus emphasize increasing C inputs, especially from slowly decomposing crop residues, and reducing soil disturbance. However these approaches are often ineffective and do not adequately reflect current views of SOC cycling, which stress the important contributions of microbial biomass (MB) inputs to SOC. We examined microbial physiology as an alternate mechanism of SOC accumulation under organic (ORG) compared to conventional (CT) agricultural management practices, where ORG is accumulating C despite fewer total C inputs and greater soil tillage. We hypothesized that microbial communities in ORG have higher growth rates (MGR) and C use efficiencies (CUE) and that this relates to greater MB production and ultimately higher retention of new C inputs. We show that ORG had 50% higher CUE (± 8 se) and 56% higher MGR (± 22 se) relative to CT ($p < 0.05$). From *in situ* ^{13}C substrate additions, we show that higher CUE and MGR are associated with greater rates and amounts of ^{13}C glucose and phenol assimilation into MBC and mineral-associated SOC pools in ORG up to 6 mo after field substrate additions ($p < 0.05$). ORG soils were also enriched in proteins and lipids and had lower abundances of aromatic compounds and plant lipids ($p < 0.05$). These results illustrate a new mechanism for SOC accumulation under reduced C inputs and intensive soil disturbance and demonstrate that agricultural systems that facilitate the transformation of plant C into MB may be an effective, often overlooked strategy for building SOC in agricultural soils.

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1. Introduction

Intensively managed agricultural systems deplete soil organic carbon (SOC), leading to potentially severe land degradation (Rajan et al., 2010), declining soil fertility (Johnston et al., 2009), and increased CO₂ emissions (Paustian et al., 1998). Traditional soil C concepts and models suggest that these trends can be reversed by increasing C inputs through additions of slowly decomposing crop residues, or by reducing C outputs by minimizing soil disturbance to slow decomposition losses (Janzen, 2006; Robertson and Grandy, 2006). Yet, in several long-term agricultural experiments, SOC accumulation rates are paradoxically higher under relatively lower

C inputs and more intensive tillage (Drinkwater et al., 1998; Gregorich et al., 2001; Marriott and Wander, 2006). Indeed, enhancing C inputs, increasing the proportion of chemically recalcitrant residue inputs, and reducing soil disturbance have all had inconsistent effects on SOC (Leifeld and Fuhrer, 2010; Pittelkow et al., 2014). These inconsistencies in SOC response to traditional soil C management practices might reflect an inadequate representation of our contemporary understanding of soil microbial controls over SOC dynamics. In contrast to traditional SOC concepts and models, emerging experimental and theoretical evidence show that dead microbial biomass (MB) (i.e. necromass) is a significant fraction of soil organic matter (SOM) (Frey et al., 1999; Grandy and Neff, 2008; Schmidt et al., 2011; Cotrufo et al., 2013; Wieder et al., 2014). If true, microbial physiological processes that regulate MB production and turnover should be strongly related to SOC accumulation (Bradford et al., 2013), and potentially under the control of management practices not exclusive to input rates and chemical recalcitrance.

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<http://dx.doi.org/10.1016/j.soilbio.2015.09.005>

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The continuous and rapid turnover of living MB can produce, over time, a considerable amount of necromass (Liang et al., 2010), now considered a key constituent of stable SOM (Simpson et al., 2007; Kindler et al., 2009; Miltner et al., 2011; Schmidt et al., 2011; Cotrufo et al., 2013; Gleixner, 2013). Although MB can be rapidly mineralized by soil organisms due to its favorable energy yield and low C:Nitrogen (C:N) ratio (Blagodatsky et al., 2000), microbial necromass and other microbial byproducts can also be selectively preserved via interactions with soil minerals and incorporation into soil aggregates (Von Lutzow et al., 2006; Heckman et al., 2013; Throckmorton et al., 2014). As a result, stable SOC pools in many soils appear to be enriched in compounds abundant in MB (e.g. lipids and proteins), but not in decomposing plant tissue (Grandy and Neff, 2008; Bol et al., 2009; Heckman et al., 2013; c.f.; Kramer et al., 2012). Given microbial necromass contributions to SOC, changes to microbial growth characteristics that affect the size, turnover rate, or biomass yield of the community may influence stable SOC accumulation via changes in the amount of MB available for stabilization (Cotrufo et al., 2013).

At the most basic level, the production of MB is governed largely by microbial physiological traits such as microbial C use efficiency (CUE) and microbial growth rate (MGR), both of which affect the rate and efficiency at which plant C is used to build MB. Microbial CUE represents the proportion of new biomass produced from substrate-C consumed, and MGR characterizes the rate of bacterial cell duplication or fungal hyphal extension over time. Both have direct influences on net MB production (Russell and Cook, 1995) and thus potentially on the rates of SOC accumulation (Bradford et al., 2013). In soils, CUE estimates range from 0.10 to 0.80 (Manzoni et al., 2012), while MGR varies from hours to weeks (Rousk and Bååth, 2011). This variability in both CUE and MGR arises from differences in the intrinsic physiology of specific bacterial and fungal species (Dethlefsen and Schmidt, 2007; Molenaar et al., 2009; Beardmore et al., 2011) and also microbial community sensitivity to the soil environment, i.e. soil temperature and resource quality (Thiet et al., 2006; Frey et al., 2013; Lee and Schmidt, 2014). At the individual species-level, variability in CUE and MGR are manifested based on differences in life history traits (Russell and Cook, 1995; Beardmore et al., 2011; Resat et al., 2012). Copiotrophic microbes, selected under resource-rich environments, are typically characterized by rapid growth rates but lower CUE relative to slower-growing oligotrophs (e.g. some fungi, actinomycetes) with a higher CUE (Fierer et al., 2007; Maharjan et al., 2007; Lipson et al., 2008; Beardmore et al., 2011). At the community-level, the manifestation of these traits will then depend on the diversity and relative abundance of active microbial species present in the community.

Even without differences in the active microbial community composition between soils, CUE and MGR can also vary depending on the soil environment. For example, assuming no changes to microbial community composition, both CUE and MGR typically increase within a microbe as resource concentrations (Eichinger et al., 2010; Roller and Schmidt, 2015) and resource quality (e.g. available free energy, or C:N) (Sinsabaugh et al., 2013) increase. An individual microbe that consumes a resource with more available free energy (e.g. low oxidation state) and nutrients (i.e. lower C:N) has more resource-C remaining for biomass synthesis after meeting their energy requirements (Gommers et al., 1988; Chiellini et al., 2007) and will lose less C to spill-over metabolism and enzyme production when nutrient limitations are minimized (Russell and Cook, 1995; Sinsabaugh et al., 2013). As such, when community-level life history traits are unchanging, labile inputs with more available energy and lower C:N ratios may theoretically encourage both a higher CUE and MGR (Eiler et al., 2003; Manzoni et al., 2012).

Agricultural management strategies that increase CUE and MGR and subsequently facilitate a faster and more efficient conversion of plant inputs to MB, may enhance stable SOC accumulation. Cover crops, which alter the overall quality and quantity of soil resource inputs, may generate this response. Often possessing low lignin concentrations and C:N ratios, cover crops should promote microbial growth and high CUE, leading to increased soil C retention. This could explain frequently reported increases in SOC with cover crops (Kallenbach et al., 2010; McDaniel et al., 2013; Tiemann et al., 2015). Examples include long-term cover-cropped agroecosystems in Pennsylvania (Drinkwater et al., 1998) and Michigan (Grandy and Robertson, 2007; Syswerda et al., 2011), where reported soil C accumulation rates were $46 \text{ g C m}^{-2} \text{ y}^{-1}$ and $50 \text{ g C m}^{-2} \text{ y}^{-1}$ despite intensive tillage and relatively fewer total soil C inputs due to lower annual net primary productivity. Here, we examine if differences in microbial physiology could be a potential mechanism for greater SOC accumulation rates under organic, cover crop management where C inputs are reduced and soil disturbance is more intense. We hypothesize that 1) distinct agricultural practices are associated with different microbial physiological growth traits; 2) cropping systems with greater CUE and/or MGR will convert relatively more new C inputs into stable microbial-derived SOC pools; and 3) management systems associated with higher CUE and MGR, and thus a potentially greater input of MB to stable SOC pools, will have a greater abundance of SOM compounds associated with MB (i.e. proteins and short-chain lipids).

2. Materials and methods

2.1. Overview

We assessed differences in microbial physiology due to agricultural management (H_1) by comparing CUE and MGR across an organic and conventional cropping system over two cropping cycles. We then examined how observed differences in microbial physiology are linked with microbial allocation of new C inputs into various SOC pools using *in situ* field additions of isotopically labeled C substrates (H_2). Finally, biomarker and soil chemistry analyses were used to relate differences in observed C allocation strategies to the abundances of SOC compounds associated with microbial-derived SOC (H_3).

2.2. Study site

We conducted our experiment at the W.K. Kellogg Biological Station (KBS) Long-Term Ecological Research Site in Hickory Corners, MI, established in 1988 (<http://kbs.msu.edu>). Following initial declines in SOC immediately after establishment, the organic cropping system at KBS has been accumulating SOC (Syswerda et al., 2011), while conventional management is maintaining or exhibiting slight losses in SOC (SI Fig. 1; Table 1). This is despite greater tillage (for weed control) and slightly lower total C inputs under organic management compared to conventional management (Table 1). The site has a mean annual precipitation of 1027 mm y^{-1} and consists of fine-loamy Kalamazoo and coarse-loamy Oshtemo soils, both Typic Hapludalfs formed on glacial till (Robertson and Hamilton, 2015). Our field experiment and soil sampling were carried out in the organic (ORG) and conventional (CT) treatments, each with six 1-ha replicated plots arranged as a complete randomized block design. Both ORG and CT treatments are under a corn-soybean-winter wheat rotation. CT is managed based on typical conventional management practices of the region, including tillage and fertilizer application rates with adjustments made based on soil tests (Robertson and Hamilton, 2015). ORG receives no chemical inputs and has a fall-planted red clover

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