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Microbial energy and matter transformation in agricultural soils

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ABSTRACT

Low bioavailability of organic carbon (C) and energy are key constraints to microbial biomass and activity. Microbial biomass, biodiversity and activity are all involved in regulating soil ecosystem services such as plant productivity, nutrient cycling and greenhouse gas emissions. A number of agricultural practices, of which tillage and fertiliser application are two examples, can increase the availability of soil organic C (SOC). Such practices often lead to reductions in soil aggregation and increases in SOC loss and greenhouse gas emissions. This review focuses on how the bioavailability of SOC and energy influence the ecology and functioning of microorganisms in agricultural soils. Firstly we consider how management practices affect the bioavailability of SOC and energy at the ecosystem level. Secondly we consider the interaction between SOC bioavailability and ecological principles that shape microbial community composition and function in agricultural systems. Lastly, we discuss and compare several examples of physiological differences that underlie how microbial species respond to C availability and management practices. We present evidence whereby management practices that increase the bioavailability of SOC alter community structure and function to favour microbial species likely to be associated with increased rates of SOC loss compared to natural ecosystems. We argue that efforts to restore stabilised, sequestered SOC stocks and improve ecosystem services in agricultural systems should be directed toward the manipulation of the microbial community composition and function to favour species associated with reduced rates of SOC loss. We conclude with several suggestions regarding where improvements in multi-disciplinary approaches concerning soil microbiology can be made to improve the sustainability of agricultural systems.

1. Introduction

Soils provide essential ecosystem functions and services such as food production, regulation of atmospheric concentrations of greenhouse gases, prevention of soil erosion, regulation of the quality and quantity of water availability, and the maintenance of animal, plant and microbial biodiversity (Ciais et al., 2013; Diaz et al., 2006; Pimentel, 2000; Tilman et al., 1997). Soil organic carbon (SOC) dynamics play a fundamental role in regulating ecosystem functions and services (Lorenz and Lal, 2014). The benefits of SOC are many and include: a source of associated essential elements for biological activity, such as nitrogen (N), phosphorus (P) and sulphur (S), collectively termed soil organic matter (SOM); improved ion exchange capacity; soil water retention; improved soil aggregation and reduced erosion; and as a sink for potential greenhouse gases (Lal, 2014). It is well documented that the conversion of native vegetation to soils used for agricultural purposes results in losses of 25–50% of SOC (Lal, 2008). Continual reductions in SOM pose a significant threat to future food security, atmospheric concentrations of greenhouse gases and biodiversity maintenance (FAO, 2015). Over the past two decades, a number of excellent reviews describing the physical and chemical factors involved in the stabilisation and turnover of SOM have been written (Baldock and Skjemstad, 2000; Cotrufo et al., 2013; Dungait et al., 2012; Schmidt et al., 2011; Sollins et al., 1996; von Lützow et al., 2007). However, a notable component lacking in these reviews has been that of microbiology, which is interesting when one considers that microbiologists were among the first to describe Earth's biogeochemical cycles (Beijerinck, 1888, 1895; Winogradsky, 1887, 1890). The purpose of this review is to better integrate concepts such as microbial ecology and physiology into the soil physico-chemistry governing SOM turnover. We aim to dispel the supposition of the soil microbial 'black box' by discussing

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several physiological properties that contribute to a cellular mechanistic basis for decreases in SOC in agricultural systems. Consequently, we address the key soil physico-chemical factors controlling SOC turnover in relatively less depth than the impact of land management practices on soil microbial ecology and physiology. We conclude by arguing that the aim of restoring stabilised, sequestered SOC stocks would be improved by considering the responses of microbial ecology and physiology to the effects of specific management practices, ideally leading to methods for the targeted manipulation of the system to favour specific phylogenetic and functional taxa.

2. Bioavailability and processing of potential energy in agricultural systems

Agricultural ecosystems across the globe are incredibly diverse in terms of edaphic and climatic properties, land use (e.g. cropping, pasture), and land management (e.g. tillage, type and quantity of fertiliser application, crop rotation, cropping intensity, mono- versus polyculture) (Matson et al., 1997; Reeves, 1997; Tilman et al., 2002; West and Post, 2002). Furthermore, there is substantial spatial variability, not only across landscapes but also with soil depth. Despite this variability, there are several characteristics which soils tend to develop after transitioning from native vegetation to agriculture, such as: a) loss of aggregate stability and increased erosion; b) acidification; c) over-supply or insufficient replacement of N and P relative to crop removal; d) changes in the molecular composition of plant biomass input; e) reductions in both composition and abundance of functional biodiversity of local plant, animal and micro-organisms; and f) SOM loss (Don et al., 2011; FAO, 2015; Flynn et al., 2009; Matson et al., 1997; Pimentel et al., 1992; Sala et al., 2000; Smith et al., 2016; Vitousek et al., 2009). Each of these has the potential to change the quantity and/or composition of SOM which is available for microbial metabolism. The predominant factor limiting the activity of heterotrophic microorganisms is the availability of organic C (Blagodatsky and Richter, 1998). For this reason, changes in organic C availability have profound consequences for soil biological processes (Schmidt et al., 2011). Fig. 1 provides a conceptual framework illustrating the interactions between the environment, SOM, edaphic properties and microorganisms which will be continuously referred to in this section.

2.1. Soil physical properties affecting SOM bioavailability

A number of soil physical properties are important in regulating SOM bioavailability for microbial metabolism, such as the rate of aggregate formation, the distribution, size and network connectivity of pore space, soil mineralogy and surface area to volume ratio of soil minerals. Aggregate formation follows a complex cycle whereby macroaggregates (>250 μm in diameter) are formed by free microaggregates (<250 μm in diameter) binding together via a combination of electrostatic interactions between clay minerals, polyvalent cations, particulate organic matter (>53 μm particle diameter, POM) and fungal mycorrhizal and root structures (Edwards and Bremner, 1967; Gupta and Germida, 2015; Tisdall and Oades, 1982). Once this occurs, new microaggregates are formed within macroaggregates as microorganisms convert encapsulated POM into ‘microbial-derived binding agents’ such as extracellular polymeric substances (EPS) necessary for biofilm formation and particle aggregation (Angers et al., 1997; Flemming and Wingender, 2010; Sandhya and Ali, 2015; Six et al., 2000a; Tisdall and Oades, 1982). Finally, the macroaggregate structure is destabilised once the original organic binding agents are sufficiently degraded, freeing microaggregates which can repeat the cycle (Six et al., 2000a). The importance of this process for regulating SOM bioavailability is made evident by physical disturbance of macroaggregates. Land management practices such as conventional tillage result in significant decreases in SOM despite similar inputs of plant biomass to non-tilled soil (Hutchinson et al., 2007; McLauchlan, 2006; Six et al., 2000a, 2000b). Aggregate integrity and SOC stocks can be recovered, at least partially, by conversion of cropping soils to pasture (Conant et al., 2001; Don et al., 2011; Gebhart et al., 1994) or by adopting no-till management practices (Reeves, 1997; West and Post, 2002). Furthermore, aggregate formation through particle flocculation can be disrupted by

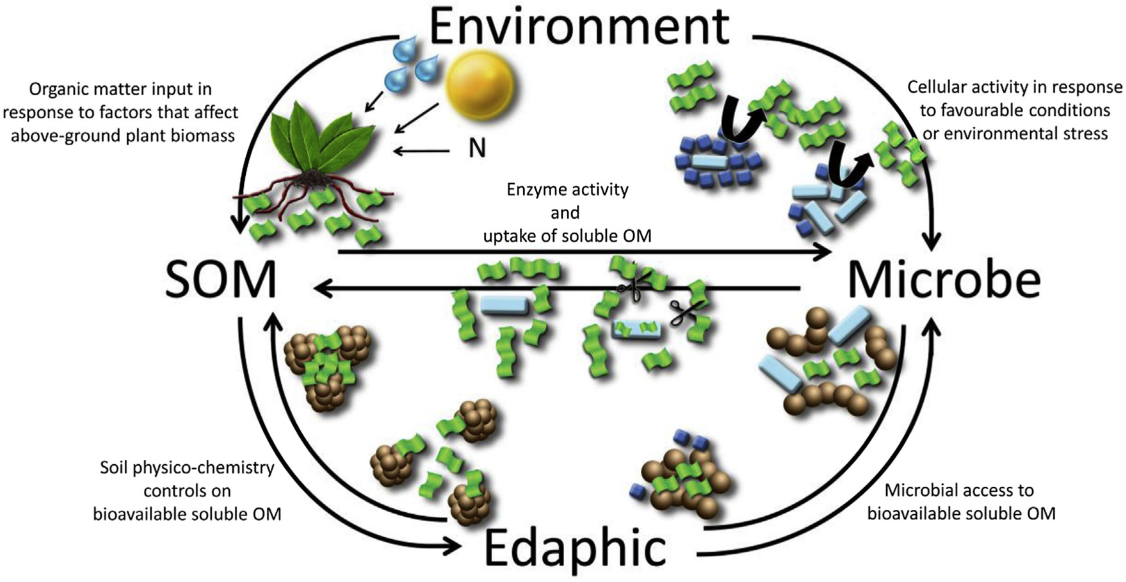

Fig. 1. A conceptual diagram of important interactions between: the environment and SOM, primarily as factors affecting plant biomass input; microorganisms and the environment, which affect cell viability and activity; SOM and microorganisms, such as relative molecular complexity of SOM; SOM and edaphic properties, including aggregate integrity controls on SOM bioavailability; and finally edaphic properties and microorganisms, such as pore size and connectivity restricting access to SOM or cell movement.