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Soil aggregate size mediates the impacts of cropping regimes on soil carbon and microbial communities

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ABSTRACT

Understanding the influence of long-term crop management practices on the soil microbial community is critical for linking soil microbial flora with ecosystem processes such as those involved in soil carbon cycling. In this study, pyrosequencing and a functional gene array (GeoChip 4.0) were used to investigate the shifts in microbial composition and functional gene structure in a medium clay soil subjected to various cropping regimes. Pyrosequencing analysis showed that the community structure (β-diversity) for bacteria and fungi was significantly impacted among different cropping treatments. Functional gene array-based analysis revealed that crop rotation practices changed the structure and abundance of genes involved in C degradation. Significant correlations were observed between the activities of four enzymes involved in soil C degradation and the abundance of genes responsible for the production of respective enzymes, suggesting that a shift in the microbial community may influence soil C dynamics. We further integrated physical, chemical, and molecular techniques (qPCR) to assess relationships between soil C, microbial derived enzymes and soil bacterial community structure at the soil micro-environmental scale (e.g. within different aggregate-size fractions). We observed a dominance of different bacterial phyla within soil microenvironments which was correlated with the amount of C in the soil aggregates suggesting that each aggregate represents a different ecological niche for microbial colonization. Significant effects of aggregate size were found for the activity of enzymes involved in C degradation suggesting that aggregate size distribution influenced C availability. The influence of cropping regimes on microbial and soil C responses declined with decreasing size of soil aggregates and especially with silt and clay microaggregates. Our results suggest that long term crop management practices influence the structural and functional potential of soil microbial communities and the impact of crop rotations on soil C turnover varies between different sized soil aggregates. These findings provide a strong framework to determine the impact of management practices on soil C and soil health.

1. Introduction

Soil carbon (C) is a key component of terrestrial ecosystems that affects the physical, chemical and biological properties of soil and contributes greatly to its functioning (Schmidt et al., 2011; Ontl and Schulte, 2012). Maintaining the balance between soil C turnover and retention of soil C is crucial because it improves soil structure, soil fertility, crop production, and ensures long-term sustainability of agricultural systems (Six et al., 2004; Reichstein et al., 2013). Furthermore, soil can play a key role in the global C cycle by acting as a sink for atmosphere CO_2 when appropriate management practices are used (Singh et al., 2010; King, 2011; Trivedi et al., 2013a,b).

In recent decades agricultural productivity has been raised by increased fertilization and pesticide application, improved irrigation, soil management regimes and crops as well as massive land use change (Tilman et al., 2002; Pittelkow et al., 2015). However, intensive agriculture has caused 30–50% losses in the amount of

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soil C in the last century leading to the degradation of various ecosystem functions (maintenance of soil structure and fertility, soil C sequestration, nutrient cycling, and hydrological services) that impact upon plant productivity and ecosystem sustainability (Thiele-Bruhn et al., 2012). Management practices such as no or minimal till, reduction or elimination of fallow periods, intensifying cropping with the use of crop rotations and cover crops, and judicious use of inputs (e.g., pesticides, irrigation, fertilizers and manures) aim at mitigating these negative impacts in order to improve sustainable production (Gomiero et al., 2011; Thiele-Bruhn et al., 2012; Pittelkow et al., 2015). Changes in land-use or management practices are known to impact soil C turnover but the underlying mechanisms are largely unknown. The lack of a mechanistic understanding constrains their broad adoption in large-scale farm management (Tscharntke et al., 2012).

In terrestrial ecosystems, the uptake of CO_2 from the atmosphere by net primary production is dominated by higher plants, but soil microorganisms contribute greatly to the ecosystem C budgets through their multiple roles in soil C dynamics thereby modifying nutrient availability and influencing the longevity and stability of C pools (Bardgett et al., 2008; Van der Heijden et al., 2008; Singh et al., 2010; Trivedi et al., 2013a,b). Management decisions in agricultural systems can be important drivers of community change for soil microbes performing important ecosystem processess including C cycling (Six et al., 2004; Postma-Blaauw et al., 2010; Pittelkow et al., 2015). Evidence suggests that terrestrial agroecosystems can be managed and manipulated to increase soil C, however how much control the soil microbial community has on C dynamics remains a debatable topic (Hartmann et al., 2015; Singh et al., 2010). Understanding the mechanisms of microbial regulation of soil C turnover is a key challenge for predicting the loss or gain of soil C under various management practices.

The functioning of soil is, to a large degree, defined by its structure which is believed to be an important regulator of microbially mediated C storage/decomposition (Mummey et al., 2006). It is believed that soil C can be physically protected either by adsorption onto organic/inorganic clay surfaces or by the entrapment in soil aggregates and is inaccessible to degrading microbes and extracellular enzymes (Six et al., 2006; King, 2011; Vos et al., 2013). Changes in agricultural management practices influence soil structural properties including soil aggregation (Six et al., 2006; Tiemann et al., 2015). This regulates soil physical and chemical heterogeneity and consequently the distribution of microbial communities and their activities among aggregates of different sizes (Vos et al., 2013). Aggregates of different sizes and stability in soil create a composite of ecological niches differing in terms of physico-chemical and structural characteristics which promotes the colonisation and maintenance of distinct microbial assemblages within each aggregate (Davinic et al., 2012; Vos et al., 2013; Tiemann et al., 2015). Knowledge of microbial communities and their activities within different microenvironments (i.e. aggregate size) is currently poor but essential for understanding the regulation of soil C cycling which has important implications for increasing crop production and maintaining agricultural sustainability (Grundmann, 2004).

Due to high microbial diversity and complexity, it remains a daunting task to link the structure and composition of soil microbial communities to the functional activities related to ecosystem functioning (Torsvik and Øvreås, 2002; Nannipieri et al., 2003; Zhou et al., 2010). In recent years various studies have provided detailed information on microbial community structure in terrestrial ecosystems (Acosta-Martinez et al., 2008; Jangid et al., 2008, 2011; Yin et al., 2010; Ramirez et al., 2012; Singh et al., 2014). However, due to the potential (or perceived) high functional redundancy, our ability to make valid linkages between the taxonomic makeup and functional potential of microbial communities such as those related to C turnover is limited (Reeve et al., 2010; Singh et al., 2010; Thiele-Bruhn et al., 2012; Nie et al., 2014). We also have a limited understanding about the potential role of soil aggregates in structuring microbial communities, and within these microhabitats, little is known about the localization of microbial communities and their functions. In the present study our aim was to identify the response of different crop types on the structure and function of soil microbial communities and the consequences for soil processes directly linked to soil C cycling. We hypothesised that: (i) the management practices would have significant impact on the structure and function of the soil microbial community linked to C turnover and these effects would be more pronounced in larger soil structures (whole soil and macroaggregates); (ii) each aggregate-size fraction would be dominated by distinct bacterial assemblages and the abundance of bacterial groups in the aggregates would depend on C availability. To test these, hypotheses we used soil samples collected from a long term "cropping regime trial" conducted on mild-clay soil in a major Cotton/Wheat producing agro-ecosystem of Australia. We first employed advanced metagenomics/molecular approaches [pyrosequencing (Margulies et al., 2005; Hamady et al., 2008); GeoChip 4.0 (He et al., 2007); qPCR (Trivedi et al., 2013b] in concert with soil biochemical [soil enzyme (Bell et al., 2013)] approaches to determine the effect of crop management on the structural diversity and functional potential of soil microbial communities in relation to indicators of soil C turnover in whole soil samples. In the second part of the study we separated the soil into three aggregate size fractions and used chemical and molecular techniques (qPCR) to access relationships between soil C, microbial derived enzymes and soil bacterial community at the soil microenvironment scale (e.g. within different aggregate-size fractions).

2. Material and methods

2.1. Field site description

The long term "Cropping System Experiment" was located in Field 6 at the Australian Cotton Research Institute, near Narrabri (149°47′ E, 30°13′ S) in New South Wales (NSW), Australia. Narrabri has a subtropical, semi-arid climate (Kottek et al., 2006) with a mild winter and a hot summer. The hottest month is January (mean daily maximum 35 °C and minimum 19 °C) and the coldest is July (mean daily maximum 18 °C and minimum 3 °C). Mean annual rainfall is 593 mm. The soil at the experimental site is an alkaline, self-mulching, gray Vertosol, classified as a fine, thermic, smectitic, Typic Haplustert (Soil Survey Staff, 2010). Mean particle size distribution in the 0–1 m depth (per 100 g) was: 64 g clay, 11 g silt, and 25 g sand.

2.2. Experimental layout and sample collection

The experiment commenced in 1998 and included four cropping treatments replicated three times. Each plot was 16 m long and 8 m wide. These treatments included: continuous cotton where cotton was grown every two years with winter fallow (C ~ C ~ C); cotton–vetch, where cotton was grown every two years in summers and vetch (*Vicia villosa* Roth) was grown each winter (CVCV); cotton–wheat where cotton was grown every two years with wheat then fallow (CW ~ CW); and cotton–wheat–vetch where cotton was grown every two years followed by wheat and vetch (CWV). The trial followed typical management practices for crops in this area i.e. cotton crop was fully irrigated while other crops received natural rainfall. Briefly cotton crops were furrow-irrigated regularly to avoid drought stress when the soil water deficit approached