Distinct respiratory responses of soils to complex organic substrate are governed predominantly by soil architecture and its microbial community

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ABSTRACT

Factors governing the turnover of organic matter (OM) added to soils, including substrate quality, climate, environment and biology, are well known, but their relative importance has been difficult to ascertain due to the interconnected nature of the soil system. This has made their inclusion in mechanistic models of OM turnover or nutrient cycling difficult despite the potential power of these models to unravel complex interactions. Using high temporal-resolution respirometry (6 min measurement intervals), we monitored the respiratory response of 67 soils sampled from across England and Wales over a 5 day period following the addition of a complex organic substrate (green barley powder). Four respiratory response archetypes were observed, characterised by different rates of respiration as well as different time-dependent patterns. We also found that it was possible to predict, with 95% accuracy, which type of respiratory behaviour a soil would exhibit based on certain physical and chemical soil properties combined with the size and phenotypic structure of the microbial community. Bulk density, microbial biomass carbon, water holding capacity and microbial community phenotype were identified as the four most important factors in predicting the soils' respiratory responses using a Bayesian belief network. These results show that the size and constitution of the microbial community are as important as physico-chemical properties of a soil in governing the respiratory response to OM addition. Such a combination suggests that the 'architecture' of the soil, i.e. the integration of the spatial organisation of the environment and the interactions between the communities living and functioning within the pore networks, is fundamentally important in regulating such processes.

1. Introduction

The rate of plant-derived organic matter decay in soil has been the subject of research for decades (Waksman et al., 1928; Jenny, 1994). However, the relative predominance of the factors governing this still remain a subject of debate (Dungait et al., 2012). Under aerobic conditions, they are considered to fit broadly into four categories: (i) substrate quality (Ågren and Bosatta, 1987), related to the ability of OM to supply both energy and nutrient elements to the decomposer community, as well as intrinsic attributes that determine the decomposability (e.g. hydrophobicity, or content of enzyme inhibiting/complexing molecules); (ii) climate (Aerts, 1997; Jastrow et al., 2006), given that all reactions are governed by thermodynamic principles, their rates rely on both temperature and moisture and are thus likely to change based on climate patterns; (iii) environment (Manzoni et al., 2012), related to the physicochemical properties of the soil (Colman and Schimel, 2013) as well as potential abiotic SOM decomposition (Kemmitt et al., 2008); (iv) soil biota (Ettema and Wardle, 2002; Dungait et al., 2012), manifest via the constitution and physiology of the microbial community and associated enzyme pools.

Despite the majority of the breakdown and turnover of OM being an inherently biological process, soil microbial communities have been largely neglected as a factor in most modelling

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frameworks until recently (Allison, 2012; Colman and Schimel, 2013; Wieder et al., 2013). Even empirical studies suggest that biology (mostly in terms of the microbial community composition) plays only a secondary role in determining the rates of these processes which are governed in large part by climate (temperature and rainfall − e.g. Aerts, 1997; Jastrow et al., 2006) and the chemistry of both the soil environment (e.g. Frey et al., 2004) and the SOM being degraded (Reed and Martiny, 2007; Makkonen et al., 2012). Determining the relationship between microbial population size or diversity and OM mineralisation has proved difficult (Fierer et al., 2007), evidenced by the apparent insensitivity of rates of OM mineralisation to changes in abundance (Jenkinson and Powlson, 1976; Garcia-Pausas and Paterson, 2011) and diversity (Garcia-Pausas and Paterson, 2011; Berthrong et al., 2013) of microbial communities. Furthermore, some current theories suggest the high energetic costs of acquiring nutrients and energy from soil OM limits the capacity of the microbial community to degrade humified material (Ekschmitt et al., 2005). Taken together, these ideas have given rise to the Regulatory Gate hypothesis (Kemmitt et al., 2008). This postulates that the disproportionately rapid rate of respiration observed after chloroform fumigation of a soil has killed off the majority of the microbial population is because the mineralisation of soil OM is a two stage process (Kemmitt et al., 2008). The first, and rate-limiting step, is abiotic and independent of microbial processes, followed by the second step where microbes are able to mineralise the small, now biologically-available, substrates. The mode of abiological conversion is not clear but could be chemical oxidation or hydrolysis, desorption from the solid phase, diffusion from pores/aggregates otherwise inaccessible to microbes, the action of extracellular enzymes or, more likely, some combination of these (Kemmitt et al., 2008). This is at odds with much of the literature, which presumes that intact microbial cells are required to turn over the majority of SOM, and where the focus is on what factors are that control the rates at which this happen (Kuzyakov et al., 2009; Paterson, 2009).

Decomposition of OM by microbial communities is highly dependent on the environmental context (extrinsic factors − those that relate to the soil as it occurs in the landscape e.g. land use, slope, and aspect). However, because soil physicochemical properties span such a wide range of variables (intrinsic factors − those which characterise soil at a specific site e.g. texture, SOM, and pH), few studies have been able to include a range of such variables simultaneously. This has led to in-depth understanding of how individual intrinsic factors such as pH (Rousk et al., 2009, 2011; Whittinghill and Hobbie, 2011) or texture (Wang et al., 2003) influence OM turnover, but offers little insight as to how these factors interact with others as part of a complex network of influences. Similarly, many studies on the effect of litter quality rely on laboratory incubations where different types of litter/substrates are added to a restricted range of soil types (e.g. Gunnarsson et al., 2008; Rinkes et al., 2014), or on reciprocal transplant experiments (Reed and Martiny, 2007) where soil types and physicochemical factors are generally not considered.

Many studies have found that the addition of carbonaceous substrates has an effect on the composition of the microbial community (e.g. Griffiths et al., 1998; Eilers et al., 2010; Pascault et al., 2013; Jagadamma et al., 2014), though only variable effects on function have been observed (Cong et al., 2015; Schimel and Schaeffer, 2012; Veen et al., 2015a,b; Zak et al., 2003). Frequent assertions are made of the so-called 'home field advantage' − the increased ability of microbes to decompose litter from their native plant communities (Ayres et al., 2009; Keiser et al., 2014; Strickland et al., 2009; Wallenstein et al., 2013) − alongside almost as many instances where this is sought but not found. When complex substrates, i.e. those comprising a variety of compounds, including

most forms of naturally-derived organic materials, are added to soils the subsequent respiratory profile is often complex (Ayres et al., 2006; Gunnarsson et al., 2008; Rinkes et al., 2014). This coupled with the observation that the *response* to added complex substrates differs between soils from different settings (Grayston et al., 2001) suggests that soil-specific OM mineralisation pathways exist, governed by combinations of biotic and abiotic system properties. This leads to questions about whether our understanding of OM cycling can be improved with a greater understanding of the impact of the size and structure of the soil microbial community (Schimel and Schaeffer, 2012) and whether this understanding can ultimately lead to improvements in earth system model performance (e.g. Schimel, 2013; Wieder et al., 2013).

The wide variation in OM quality and quantity, the impact of multiple environmental conditions, and inherent variation in microbial processes, contribute to the significant difficulty in unravelling the importance of microbial communities to OM decomposition, and subsequently how their effect into models of terrestrial C-cycling. The overarching purpose of this work was to assess the short term ability of extant microbial communities, in a diverse range of soils, to process inputs of a plant-derived complex organic substrate. This will aid our understanding of the relationship between microbiota, the combination of intrinsic and extrinsic factors making up the soil environment, and the manner in which OM is mineralized by such communities.

We hypothesized that on addition of a complex organic material (i) distinct respiratory response patterns would be manifest in different soils arising from their variety of intrinsic and extrinsic factors, (ii) such responses would be related to combinations of particular factors rather than being driven by individual factors and, (iii) because CO_2 release from soils is an intrinsically biological process, the size and structure of the microbial community would be the key factors in determining the respiratory response to additions of OM.

2. Methods

2.1. Sample collection and preparation

Sites were identified through a random stratified subsample of the 677 locations of the National Soil Inventory (NSI) of England and Wales (McGrath and Loveland, 1992) based on prior information about pH and carbon content of soils. Sites were categorised as high, medium and low pH (low<6.5, medium 6.5–7.5 and high >7.5), then further as high, medium and low carbon contents (low<1.65%, medium 1.65−2.55%, and high >2.55%), resulting in 9 categories of site; final selection for sampling was based on location and permission to access land being granted. Corstanje et al. (2015) found that to successfully determine the relative importance of factors to soil processes, using Bayesian modelling, it was critical to have data on soil properties (both intrinsic and extrinsic) cover as wide a range of values as possible. For this reason within field variability was not considered (samples were pooled as described later) so that samples could be collected from a large number of sites instead. Sixty-seven sites were sampled (see Table S1 for details) by collecting 25 cores (3.5 cm diameter by 10 cm depth) in a grid pattern over a 25 m^2 area. Three further samples were collected from the centre of the sampling grid at each site and their bulk density determined. Site-specific information about land use, length of land-use, slope and aspect (extrinsic factors) was also collected. The 25 cores were pooled and taken as representative of the site, transported to the laboratory and stored at 4 °C until processing (as was done for the NSI). Pooled samples were sieved to pass a 2 mm mesh screen and a subsample was dried at 105 °C for 48 h to determine moisture content. The water holding capacity