



Metabolising old soil carbon: Simply a matter of simple organic matter?



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ABSTRACT

Bare fallow soils that have been deprived of fresh carbon inputs for prolonged periods contain mostly old, stable organic carbon. In order to shed light on the nature of this carbon, the functional diversity profiles (MicroRespTM, BiologTM and enzyme activity spectra) of the microbial communities of long-term bare-fallow soils were analysed and compared with those of the microbial communities from their cultivated counterparts. It was assumed that the catabolic and enzymatic profiles would reflect the type of substrates available to the microbial communities. The catabolic profiles suggested that the microbial communities in the long-term bare-fallow soil were exposed to a less diverse range of substrates and that these substrates tended to be of simpler molecular forms. Both the catabolic and enzyme activity profiles suggested that the microbial communities from the long-term bare-fallow soils were less adapted to using polymers. These results do not fit with the traditional view of old, stable carbon being composed of complex, recalcitrant polymers. Microbial communities from the long-term bare fallow soils tended to preferentially use substrates with higher nominal oxidation states of carbon relative to the substrates used by the microbial communities from the cultivated soils. This suggests that the microbial communities from the long-term bare-fallow soils were better adapted to using readily oxidizable, although energetically less rewarding, substrates. Microbial communities appear to adapt to the deprivation of fresh organic matter by using substrates that require little investment, such as enzyme production.

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1. Introduction

The mean residence time, i.e. the inverse of the decomposition rate, of soil organic carbon (SOC) is extremely variable, ranging from a few days to several centuries or even millennia (Trumbore, 1997; Jenkinson et al., 2008). These differences reflect a combination of the intrinsic decomposability of the C and the environmental constraints on decomposition (Schmidt et al., 2011). The old organic C in soil has generated much interest because it represents the majority of SOC and the stability of this C is uncertain, in particular when faced with external perturbations, such as climate change or changes in land management (e.g. Fang et al., 2005;

Reichstein et al., 2005; Davidson and Janssens, 2006; Hartley and Ineson, 2008). Although this C is treated as one or two homogeneous pools in most C dynamics models, i.e. the old pool in ICBM (Andrén and Kätterer, 1997), the slow and passive organic C in the Century model (Parton et al., 1987) or the humus and inert pools in the RothC model (Jenkinson and Rayner, 1977), it is likely that it is made up of a diverse range of organic compounds that are stabilised through a range of different mechanisms. The different organic compounds that constitute SOC have (i) different inherent kinetic properties (Davidson and Janssens, 2006), (ii) display differential adsorption to mineral surfaces (Kleber et al., 2007), (iii) are more or less accessible to enzymes catalysing their degradation (Ekschmitt et al., 2005) or (iv) their decomposition rates are constrained by the physiology of the decomposer populations (Ekschmitt et al., 2005; German et al., 2011). If accurate predictions of the response of SOC to external perturbations are to be obtained,

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then a clear understanding of these mechanisms is required (Conant et al., 2011). However, progress in this area has been hampered by a poor understanding of the nature of the molecular compounds that constitute the old, stable organic C in soil.

Long-term bare fallow field trials are interesting with regard to the study of old SOC as much of the C with short residence times has been mineralised during the bare-fallow period. Previous studies on long-term bare fallow soils have shown that the C in soils that have been subjected to bare fallow management for more than 60 years is almost entirely in the form of stable C, i.e. C that is hundreds or thousands of years old (Barré et al., 2010): the old C has been, to a certain extent, isolated by microbial decomposition processes that occurred naturally during the bare-fallow period. The diversity of microbial communities from long-term bare-fallow soils is not believed to be reduced by the long-term deprivation of fresh organic matter (Paterson et al., 2011; Hirsch et al., 2009). However, the data related to the functional diversity of these communities is not consistent: some studies have indicated that the functional diversity is unaffected (Hirsch et al., 2009; Guenet et al., 2011), but others have shown that the capacity to degrade certain compounds is diminished (Paterson et al., 2011).

Microbial communities adapt to the substrate that is available to them. There is a tight link between microbial communities, their immediate environment and the resources available to them: biogeographic studies have shown that microbial communities are mainly influenced by local environmental properties (e.g. Fierer and Jackson, 2006) and the experimental evolution of microorganisms has shown that they adapt rapidly and increase their fitness towards the available substrate in simple and complex environments (Lenski et al., 1991; Barrett et al., 2005). It has also been shown that bacteria do not lose the ability to grow on substrate to which they have not been exposed for many generations, but that they generally perform less well than lines evolved on the substrate (MacLean and Bell, 2002). Finally, relationships between the activity profiles of microbial communities and the composition of soil organic matter across a range of soils have been identified (Grandy et al., 2009).

Old C is difficult to isolate from soil as the C is not neatly compartmentalised. Traditionally, old, stable C has been viewed as being chemically recalcitrant, made up of large, complex macromolecules (Stevenson, 1994). This view of stable organic matter is sometimes referred to as the “polymer model” of soil organic matter. However, recent research suggests that the stability of old C in soil is the result of a combination of physicochemical and biological factors that reduce the rate at which old C is decomposed rather than the result of the intrinsic molecular properties of the C (Schmidt et al., 2011). For example, Near Edge X-Ray Absorption Fine Structure spectroscopy analyses have suggested that older C (measured as ^{14}C age) can contain a greater proportion of easily metabolisable molecules than younger C (Kleber et al., 2011). Distinct differences in the relative abundances of various chemical groups between one of the long-term bare-fallow soils (Ultuna) included in this study and the same soil having received some form of organic input have also been identified (Gerzabek et al., 2006).

Based on these insights, it was hypothesised that the functioning (i.e. enzymatic spectra and catabolic capacities) of microbial communities from long-term bare-fallow soils would be adapted to using simple, labile substrates rather than complex substrates. The reasons for testing this hypothesis were twofold. The first was to search for corollary evidence that old SOC contains proportionally more simple, readily metabolisable, substrates than old SOC (Kleber et al., 2011) or that complex polymers in old C are simply not available to or used by soil microbial communities. In the present paper, we used the microbial communities as “biological *in situ* probes” of the organic matter. The second reason was to document

how the functional diversity of microbial communities changed when deprived of fresh plant organic matter inputs for prolonged periods. The hypothesis was tested by comparing the catabolic profiles and enzymatic spectra of microbial communities from four long-term bare-fallow soils and from their cultivated counterparts. It was expected that catabolic profiles of the microbial communities from the long-term bare-fallow soils would display a more pronounced preference for simple substrates and would be less capable of using complex molecules than their counterparts from cultivated soils. However, the bare-fallow soils were not expected to completely lose the capacity to metabolise complex or plant derived compounds. It was also expected that the enzyme activity profiles of the long-term bare-fallow soils would contain relatively more enzymes targeting simple molecules.

2. Material and methods

2.1. Soils

In spring 2010, samples were collected from four long-term bare fallow sites (Versailles, France – 48°48 N, 2°08 E; Grignon, France – 48°51 N; Ultuna, Sweden – 59°49 N, 17°38 E; Lanna, Sweden – 58.34°N, 13.10°E) and their cultivated counterparts and all samples were stored at 4 °C until use. The bare-fallow plots at the sites had received no C inputs, except from occasional algae and weed growth despite repeated weeding, for between 82 and 14 years. Soil characteristics of the four sites are given in Table 1. Three replicate plots were sampled at all the sites. Prior to analysis, all soils were sieved <2 mm and incubated at 20 °C for two weeks at 45% water holding capacity (WHC).

2.2. Catabolic profiles

Catabolic profiles were constructed for all the soils using Biolog EcoPlates™ (Biolog Inc., Hayward, CA, USA) and for three of the soils using the MicroResp™ system (Campbell et al., 2003). The Grignon soil contained carbonates and therefore reliable MicroResp profiles could not be established. The MicroResp profiles were established using 22 substrates belonging to 6 different molecular families (Table 2). Here, substrates were dissolved in deionised water (30 mg C per mL soil water) and dispensed at a rate of 30 µL solution per well, bringing the water content of the soils to 55% water holding capacity. Due to the low solubility of xylan, protocatechuic acid, fumaric acid and glycogen, these were added in powder form at a rate of 30 mg C per mL soil water after mixing with 100 mg talcum powder g^{-1} dry weight equivalent soil. The samples that were amended with substrate and talcum powder also received 30 µL deionised water. Both CO_2 evolved from water amended soils and from the soil after talcum powder and water

Table 1

Basic characteristics of the soils from the four long-term experimental sites (Versailles and Grignon in France and Ultuna and Lanna in Sweden).

Soil	Soil C (%)	Soil N (%)	C-to-N ratio	pH (H ₂ O)
Versailles ^a fallow	0.56	0.06	9.4	4.4
Versailles ^a cultivated	1.45	1.20	11.9	6.8
Grignon ^b fallow	0.86	0.09	9.6	8.3
Grignon ^b cultivated	1.11	0.11	9.8	8.3
Ultuna ^b fallow	0.97	0.10	9.7	6.1
Ultuna ^b cultivated	1.12	0.11	10.2	6.2
Lanna ^c fallow	1.89	0.14	13.5	6.4
Lanna ^c cultivated	1.96	0.15	13.1	6.4

^a Field site established in 1928.

^b Field site established in 1956.

^c Field site established in 1996.

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