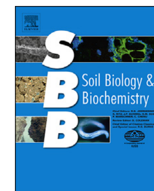
Soil Biology & Biochemistry 109 (2017) 59–69

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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



Temperature sensitivity of substrate-use efficiency can result from altered microbial physiology without change to community composition

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ARTICLE INFO

Article history:
Received 17 November 2016
Received in revised form
3 February 2017
Accepted 6 February 2017

Keywords:
Carbon-use efficiency
Thermodynamic efficiency
Microbial community composition
Temperature sensitivity
Substrate quality
Isothermal calorimetry

ABSTRACT

Mechanisms controlling carbon stabilisation in soil and its feedback to climate change are of considerable importance. Microbial substrate-use efficiency is an important property during decomposition of soil organic matter. It determines the allocation of substrate towards biosynthetic stabilisation of carbon and for respiratory losses into the atmosphere. Previously, it was observed that substrate-use efficiency declines with an increase in temperature and that it varies across organic substrates. Yet, our mechanistic understanding of processes causing the temperature sensitivity of substrate-use efficiency is limited. Changes in substrate-use efficiency could be triggered by (i) shifts in the active components of microbial communities, (ii) changes in microbial physiology within the same community, or (iii) a combination of both. In the present study, we evaluated the link between microbial community composition and substrate-use efficiency, combining measurements of carbon mineralisation and microbial energetics. We found only minor shifts in microbial community composition, despite large differences in substrate-use efficiencies across incubation temperatures and substrate additions. We conclude that short-term changes in substrate-use efficiency were mainly caused by changes in microbial physiology, but emphasize that future studies should focus on resolving long-term trade-offs between physiological and community influences on substrate-use efficiency.

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1. Introduction

Global soil carbon (C) stocks exceed atmospheric C by more than three times and above-ground biomass C by more than four times (Ciais et al., 2013). In light of predicted climate change, the balance between soil C sequestration and soil organic C decomposition is of considerable importance (e.g. Allison et al., 2010; Davidson and Janssens, 2006; Melillo et al., 2002). During microbial decomposition of soil organic matter (SOM), organic C is allocated for respiratory energy production and towards biosynthetic stabilisation such as cell maintenance and growth. This partitioning (microbial substrate-use efficiency) is often assumed to be a constant in process-based models (e.g. Coleman and Jenkinson, 1996; Parton et al., 1987). Some studies (e.g. Dijkstra et al., 2011; Frey et al., 2013; Hagerty et al., 2014) confirm this assumption when glucose was used as a substrate across various incubation temperatures. In contrast, studies using a range of substrates (e.g. Devêvre and Horwáth, 2000; Frey et al., 2013) and theoretical models (Manzoni et al., 2012; Sinsabaugh et al., 2013) suggest that substrate-use efficiency is temperature dependent, decreasing with increasing temperature. In theory, the decrease is caused by differing temperature sensitivities of microbial respiration and substrate uptake (Manzoni et al., 2012). Still, our mechanistic understanding of the underlying processes is limited. Changes in substrate-use efficiency with temperature may be caused by (i) physiological changes within the microbial community actively processing substrates, (ii) shifts in the composition of the active community, or (iii) a combination of both (Manzoni et al., 2012; Schimel and Schaeffer, 2012).

Microbial substrate-use efficiency is a critical physiological

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http://dx.doi.org/10.1016/j.soilbio.2017.02.005
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property in the terrestrial C cycle. At the microbial community level, it could be affected by functional traits and life history strategies (Schimel and Schaeffer, 2012). Recently, positive correlations were observed between efficiency and the abundance of Gram-negative bacteria (Bölscher et al., 2016; Harris et al., 2012) indicating that they may play an important role for varying substrate-use efficiencies across communities. Furthermore, fungi are commonly assumed to utilise substrate with higher efficiency than bacteria (e.g. Holland and Coleman, 1987; Ohtonen et al., 1999). This idea has been around for some time, but although some studies support this notion (Bölscher et al., 2016; Kallenbach et al., 2016), others do not (Brant et al., 2006; Thiet et al., 2006). Seasonal dynamics in microbial community composition, with a shift towards increased relative abundance of fungi in winter, have been observed (Buckeridge et al., 2013; Schadt et al., 2003). Such a shift towards relatively more active fungi at lower temperature may be an explanation in observed increase in efficiencies with lower temperatures. Yet, few studies complemented direct measurements of substrate-use efficiency across temperatures with investigations of community composition.

Estimates of microbial substrate-use efficiency often rely on quantification of ^{13}C in microbial biomass after uptake of labelled substrate. The fumigation-extraction method (Vance et al., 1987) is commonly used for this evaluation, but may not be wholly reliable shortly after substrate addition (Marstorp and Witter, 1999; Witter and Dahlin, 1995). Recently, we proposed a microbial energetics approach using isothermal calorimetry to quantify substrate-use efficiency (Bölscher et al., 2016; Harris et al., 2012). We suggested the determination of thermodynamic efficiency by adapting the equations of Battley (1987, 1960). This approach does not rely on measurements of substrate incorporation into microbial biomass by fumigation-extraction. Microbial energetics approaches quantify net metabolic heat production which covers all metabolic processes and not only those leading to CO_2 production making them complementary to respiratory-based investigations (Herrmann et al., 2014). Here, we combine energetics and respiratory approaches to compare results from both.

The aim of the present study was to investigate links between changes in microbial community composition and temperature sensitivity of substrate-use efficiency. The hypothesis in the present study was that temperature sensitive microbial substrate-use efficiencies are linked to shifts in the composition of the active microbial community. To test this hypothesis, we analysed substrate-use efficiency in two contrasting soil treatments at two temperatures by complementing substrate induced respiration using isotopic ^{13}C-labelling with microbial energetics determined via isothermal calorimetry. A set of substrates was used as previous research has shown that temperature sensitivity of microbial substrate-use efficiency is substrate dependent (Frey et al., 2013).

2. Material and methods

2.1. Soils

Soil samples were collected at the Pilmore soil cultivation experiment (56°27′N, 03°04′W, the James Hutton Institute, Dundee, UK), on a freely-drained Dystric-Fluvic Cambisol (IUSS, 2006) with a sandy-loam texture (Griffiths et al., 2010). The site was established in 2005 and was exposed to a maritime climate with an average annual air temperature of 8.3 °C (12 °C at time of sampling) and precipitation of 720 mm (30 year average, Ghee et al., 2013). Additional soil properties are given in Table 1. Soil treatments consisted of different organic amendments in three split-plot randomised field replicates. Sampled plots received either (i) compost amendments at an annual rate of 35 t/ha (Compost) or (ii) cropped control plots were without organic amendments (Unamended). Spring barley is grown annually on all plots. Soil was collected from 5 to 15 cm depths after removal of barley stubbles in October 2014. Samples from three field replicates were pooled into one composite sample to achieve samples that were representative of field treatments while minimising influences of plot variation. The study focused on fundamental understanding of temperature effects on substrate-use efficiency and therefore small variation among samples was of importance. Samples were sieved to 2 mm, visible plant fragments and macro fauna removed, and water contents were adjusted to 45% water holding capacity. The samples were divided into sub-sets and frozen until further analysis to supress microbial activity as all measurements could not be carried out simultaneously. One sub-set was used to investigate C mineralisation, another for determination of microbial energetics. For each experimental treatment, three laboratory replicates were used from each composite sample.

2.2. Incubation experiments

2.2.1. Carbon mineralisation

Soil samples were thawed and incubated at 20 °C for two days to allow the initial respiratory flush upon freeze-thawing to subside (Herrmann and Witter, 2002). The samples were then pre-incubated at either 5 or 20 °C for ten days. The 10-day pre-incubation was based on previous observations (Cookson et al., 2007) indicating that short-term time intervals should be sufficient for altering microbial community composition at temperatures similar to the present study.

For each temperature, field treatment and laboratory replicate, aliquots (30 g dry weight) were weighed into plastic jars, pre-incubated and soils then received 4.16 μmol C g^{-1} soil of either D-glucose, D-trehalose, L-alanine, or phenol. Control samples received ultrapure water. Substrate solutions contained a mixture of unlabelled and 99 atom % ^{13}C uniformly-labelled substrate resulting in a final enrichment of 4.9–5.5 atom-% ^{13}C. Substrate additions adjusted the water content of soils to approx. 55% water holding capacity. Samples were placed into gastight 0.58 l Kilner jars and headspaces were purged with CO_2 free air until the CO_2 concentration was below 4 ppm. The soils were incubated for 24 h at the experimental temperatures of 5 or 20 °C and headspace gas samples were taken after 6, 12 and 24 h and analysed as described below. After each sampling, the headspace was again purged with CO_2 free air. At the end of the incubation period, soil samples were thoroughly homogenised and split for analysis of microbial biomass C and phospholipid fatty acid (PLFA) profiles (see below).

2.2.2. Microbial energetics

Heat production from substrate utilisation was measured in a parallel experiment, maintaining experimental conditions as described above. Replicate soil aliquots (5 g dry weight) were placed into 20 ml glass reaction vials and vials were sealed with an admix ampule system (TA Instruments, New Castle, DE, USA; Bölscher et al., 2016). Each admix ampule contained either D-glucose, D-trehalose, L-alanine, phenol or ultrapure water as control. The samples were introduced into a TAM Air isothermal calorimeter (TA Instruments, New Castle, DE, USA) set to 5 or 20 °C. After an equilibration time of 7 and 4 h (5 and 20 °C, respectively), substrate solutions were added dropwise, providing 4.16 μmol C g^{-1} soil which increased the water content to approx. 55% water holding capacity. Thermal energy production rates were recorded continuously over 24 h. At the end of the incubation, concentration of CO_2 in the headspace was analysed by gas chromatography (Clarus 500 GC, Perkin Elmer Arnel, Waltham, MA, USA) to ensure that the two parallel incubation experiments were consistent,

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