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Shifts in the microbial community structure explain the response of soil respiration to land-use change but not to climate warming

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ABSTRACT

Soil stores more carbon (C) than plants and atmosphere combined and it is vulnerable to increased microbial respiration under projected global changes including land-use change and future climate scenarios (mainly elevated temperature). Land-use change is known to have a direct impact on soil organic C and soil respiration (Rs) but the mechanisms that drive these changes remain debatable. Similarly, recent studies and simulation models predict that Rs will respond positively to projected climate warming. However, there are significant uncertainties in the magnitude and mechanisms of this feedback response of Rs to global change. To identify the mechanisms of Rs response to land-use change and climate warming, we first investigated Rs from different land use types. Soil respiration was estimated seasonally from four different Scottish land uses: moorland, birch woodland, grassland and pine forest ($n = 24$). Our results demonstrated that despite a dramatic loss of total C and nitrogen (N) in the soils under birch trees, the Rs in the birch woodland was similar to that of the moorland and pine forest, with Rs in the grassland being significantly higher. The microbial community structure, estimated by Multiplex Terminal-Restriction Fragment Length Polymorphism (MT-RFLP) and 454 pyrosequencing, was significantly different under each land use type. A strong correlation of Rs with soil properties (pH, inorganic N, C:N ratio and moisture) and with microbial community structure was identified.

To test the impact of elevated temperature on Rs and to identify potential microbial mechanisms, we performed laboratory incubation studies. Soils from different land uses were incubated at 7 °C (mean annual temperature (MAT) in Scotland) and 10 °C (MAT + 3 °C) with and without the presence of a labile (^{13}C-glucose) and recalcitrant (^{13}C-lignin) form of C to identify the active groups of microbes and to determine the role of substrate availability on feedback response. The warming treatment induced an increase in Rs rates in all soils. The magnitude of the Rs response to warming was modulated by the land use types, and the Rs was more prominent in soils with high C contents. The addition of glucose substantially increased both total and rate of Rs compared to no substrate- and lignin-amended soils, providing evidence of labile C depletion as a mechanism for the thermal response of Rs. The warming treatment did not impact the composition of the active or total microbial community as revealed by phospholipid fatty acid-stable isotope probing (PLFA-SIP), MT-RFLP and 454 pyrosequencing. Our results showed that the microbial metabolic activity was higher under warming treatment suggesting that a positive feedback of Rs to increased temperature is mediated by changes in substrate availability and microbial metabolic rates.

1. Introduction

Soil stores 2500 Pg of carbon (C) which is significantly more than the C locked in the plant and atmospheric pools (Singh et al., 2010). Soil microbial respiration (Rs) emits ~60 Pg annually from

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the soil organic carbon (SOC) pool, which is compensated by plant photosynthetic activities (Bradford, 2013). This balance is vulnerable to global change, including land-use change and climate warming, resulting in higher rates of Rs thereby increasing the atmospheric concentration of CO_2. Currently, there is a strong global trend towards the afforestation of marginal land, driven by a high demand for timber and the potential for forests to sequester atmospheric CO_2. Land-use change can potentially have a significant impact on Rs through its influence on microclimate, soil abiotic and biotic properties. For example, previous studies found low microbial biomass and Rs following conversion of pasture into forest (Ross et al., 2002; Scott et al., 2006). However, the direction, magnitude and mechanisms of Rs response to land-use change remain controversial (Barger et al., 2011; Zhang et al., 2013). Land-use change can have a significant direct impact on soil microbial communities, which are the main components of Rs, *via* a transfer and shift in quality and quantity of photosynthates and litter. Indirectly, land-use change can impact microbial communities *via* a shift in soil abiotic properties such as moisture, porosity and nutrient availability (Macdonald et al., 2009). However, we have little mechanistic knowledge of the response of the various components of microbial community (biomass, structure and diversity) to land-use change, and the consequences for Rs. Identifying the key microbial mechanisms is important for understanding the specific effect of land-use change on Rs.

Current soil carbon and Earth-system models estimate a positive and exponential feedback loop of Rs in response to global warming (Friedlingstein et al., 2006). This assumption is supported by short-term experiments which have demonstrated an exponential relationship between Rs and increasing temperature (Davidson and Janssens, 2006). However, there are significant uncertainties regarding the feedback response and it is proposed that, like plant and animal metabolisms, microbial respiration can acclimatise to a global increase in temperature despite a current debate in the literature (Hartley et al., 2007; Brabford et al., 2008; Bradford, 2013; Karhu et al., 2014; Wei et al., 2014). For example, Bradford et al. (2008, 2010) reported acclimation of soil respiration even in the presence of sufficient substrate availability, suggesting that the microbial community was able to adjust its metabolic activities to increasing temperature. However, other studies reported no acclimation of Rs (Hartley et al., 2007, 2008; Vicca et al., 2009) and argued that the increasing Rs response to temperature was linked to substrate depletion. Recent studies also described a potential role of shifts in the soil microbial biomass or community structure in Rs thermal response (Thiessen et al., 2013; Wei et al., 2014). Such contrasting observations preclude the development of a general explanatory mechanism for Rs response to climate warming. Understanding both magnitude and mechanisms is important to reduce the uncertainties in the predicted 40% increase in Rs feedback response associated with climate warming (Stocker et al., 2013).

A recent study conducted across the globe concluded that soils with high C contents and from cooler parts of the world are more vulnerable to C loss under global warming (Karhu et al., 2014). The authors also reported that rather than acclimation, most soils showed an enhanced response to climate warming. This was more pronounced in temperate and boreal ecosystems which store more than 50% of terrestrial C. However, there are still significant knowledge gaps on the mechanisms of Rs response to predicted global warming. Several mechanisms that can determine the temperature sensitivity of Rs have been proposed, including: (1) loss of labile C (substrate depletion theory), (2) change in microbial physiology, (3) change in microbial community composition, or (4) decrease in carbon-use efficiency in the microbial community. In modelling studies, it was suggested that Rs acclimation can be explained by a single factor of substrate depletion (Kirschbaum, 2004; Knorr et al., 2005). One aspect that received less attention is substrate origin. Because soil C is a direct product of the decomposition of plant debris, it is expected that different land uses will result in soil C compounds which differ in their structure and composition (C quality). Invariably, microbial community structure, which is a key regulator of Rs, is altered under land-use change (Costa et al., 2006; Macdonald et al., 2009). Because two key components of the Rs response to temperature are proposed to be substrate quality and microbial community composition/biomass (Hartley et al., 2007; Bradford et al., 2008; Singh et al., 2010), it can be predicted that Rs from different land uses will respond differently to climate warming.

Our aim was to investigate the mechanism(s) that can best explain the Rs response to land-use change and climate warming under carbon-rich ecosystems. To test this, we first investigated the impact of land-use change on Rs and hypothesised that changes in the microbial community structure will explain the Rs response to afforestation. We then carried out incubation studies in order to identify the mechanism(s) which could explain the temperature sensitivity of Rs in the presence and absence of additional labile (glucose) or recalcitrant (lignin) substrates. We hypothesised that both substrate availability and microbial community (biomass, structure and/or physiology) response will be linked to the temperature sensitivity of the soil C. We examined the temperature sensitivity of Rs from different land uses to address key questions: whether Rs acclimatises and which mechanism(s) (substrate availability and/or microbial acclimation) best explains Rs response to climate warming.

2. Material and methods

2.1. Field sites and soil sampling

The soils and sites used in this experiment were part of a bigger seasonal project and a detailed description can be found elsewhere (Nazaries et al., 2013). In brief, three sites were selected (Craggan, Glensaugh and Tulchan, Scotland). The land-use changes investigated were (i) moorland colonisation/afforestation by (old) birch woodland (Craggan and Tulchan) and (ii) afforestation of grassland with pine trees (Glensaugh). Soil samples (12 replicates per land use) were carefully excavated using 10-cm wide stainless steel rings over a 0–10 cm profile. The soil cores were kept intact inside the sampling rings, wrapped in cling film and brought back to the laboratory, where they were placed in a controlled-environment room (70% humidity, no light) and incubated for 24 h (without the cling film) at a temperature close to the site's air temperature at the time of sampling: 5 °C in winter, 10 °C in spring, 15 °C in summer and 20 °C in autumn (see Nazaries et al. (2013) for more details). Headspace CO_2 concentration (considered soil respiration – Rs) and microbial communities were measured seasonally. The chemical soil properties were measured in autumn 2008 and summer 2009 (pH, total C and N, NH_4^+ and NO_3^- content and soil moisture) while the physical soil properties were only measured in summer 2009. For the temperature sensitivity incubation of the present study, only the soils sampled in summer 2009 were used.

2.2. Soil respiration (Rs) measurements

Headspace gas samples were taken using closed-bottom PVC chambers (~9 L) fitted with a gas sampling tube and a 3-way tap. Out of the 12 replicates from each land use, three soil cores per chamber were used, with four chambers for each land use (n = 4). Two supplementary chambers containing no soil cores were also used in order to detect the level of "background flux", in other