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Microbial dormancy promotes microbial biomass and respiration across pulses of drying-wetting stress

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ABSTRACT

Recent work suggests that metabolic activation and deactivation of microbes in soil strongly influences soil carbon (C) dynamics and climate feedbacks. However, few soil C models consider these transitions. We hypothesized that microbes' capacity to enter and exit dormancy in response to unfavorable and favorable environmental conditions decreases the sensitivity of microbial biomass and cumulative respiration to environmental stress. To test this hypothesis, we collected data from a rewetting experiment and used it to design and parameterize dormancy in an existing microbe-based soil C model. Then we compared predictions of microbial biomass and soil heterotrophic respiration (R_H) under simulated cycles of stressful (dryness) and favorable (wet pulses) conditions. Because the influence of moisture on microbial processes in soil generally depends on temperature, we collected data and tested predictions at different temperatures. When dormancy was not taken into account, simulated microbial biomass and cumulative microbial respiration over five years were lower and decreased faster under lengthening drying-wetting cycles. Differences due to dormancy increased with temperature and with the length of the dry periods between wetting events. We conclude that ignoring both the capacity of microbes to enter and exit dormancy in response to the environment and the consequences of these metabolic responses for soil C cycling results in predictions of unrealistically low R_H under warming and drying-wetting cycles.

1. Introduction

Changes in global climate such as warming and altered precipitation patterns (Stocker, 2014) will trigger carbon (C) cycle feedbacks with the capacity to either accelerate or slow climate change. Global soil respiration (R_S), the second largest terrestrial carbon flux to the atmosphere (~70 Pg C y^{-1}; Raich and Schlesinger, 1992), has been increasing with temperature (~3.3 Pg C y^{-1} $°C^{-1}$) over the observational record of approximately 5 decades (Bond-Lamberty and Thomson, 2010; Hashimoto et al., 2015). R_S responses to warming are influenced by soil moisture. Although warming generally increases R_S (Bond-Lamberty and Thomson, 2010; Hashimoto et al., 2015), prolonged droughts can offset the effects of warming on R_S (Schindlbacher et al., 2012; Suseela et al., 2012). In many areas of the world, rainfall events are becoming less frequent and more extreme (Stocker, 2014). In order to predict future changes in R_S and their potential to accelerate climate change, we need to understand the mechanisms that control the responses of R_S to climate. Generally 50–70% of R_S is produced by microbial decomposers (i.e. heterotrophic respiration, R_H), with the rest coming from plant roots and root-associated microbes (i.e. autotrophic respiration, R_A) (Bond-Lamberty et al., 2004). Therefore, understanding the ways in which microbes respond to changes in temperature and moisture is a critical step towards developing the modeling tools needed to predict soil C-climate feedbacks.

Earth system models (ESMs), which couple terrestrial C cycling (including soils) to other components of the global carbon cycle-climate system, are powerful tools for predicting global and regional changes in biogeochemistry and climate. However, much uncertainty remains as to the magnitude and even direction of carbon cycle feedbacks to climate. Predictions from the Coupled Model Intercomparison Project Phase 5 (CMIP5) suggest that by 2100, terrestrial ecosystems could act as either a global C sink or a source (Friedlingstein et al., 2014). None of these ESMs explicitly represented microbial processes in soil. Microbes play a major role in regulating the global C cycle (Schimel et al., 2007; Allison et al., 2010; Wieder et al., 2013), and the use of soil C models that explicitly represent microbial processes (i.e. 'microbial-explicit'

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models) is being increasingly explored as an approach that could reduce uncertainty in predictions of terrestrial C cycle-climate feedbacks (Todd-Brown et al., 2012; Treseder et al., 2012; Wieder et al., 2015). Microbial-explicit models generally include a single pool representing total microbial biomass, which is used to predict extracellular enzyme production or decomposition of soil organic matter. However, a large proportion of microbes in soil is generally metabolically inactive or dormant (Lennon and Jones, 2011). Under this state, microbes almost entirely reduce production of extracellular enzymes and all metabolic activities related to decomposition (Blagodatskaya and Kuzyakov, 2013). Generally, less than 10–20% of microbes in soil are metabolically active and capable of driving soil biogeochemical processes (Lennon and Jones, 2011).

Metabolic activation and deactivation of microbes in soil can affect R_H (Placella et al., 2012; Aanderud et al., 2015; Barnard et al., 2015). Activation of dormant cells has been used to explain pulses of R_H after wetting dry soils (a phenomenon known as the Birch effect; Birch, 1958) in a variety of ecosystems, including grasslands (Bottner, 1985; Alvarez et al., 1998; Placella et al., 2012; Aanderud et al., 2015; Barnard et al., 2015), forests (Aanderud et al., 2015; Salazar-Villegas et al., 2016), and agricultural fields (Aanderud et al., 2015). The pulses of R_H that follow wetting of dry soils can contribute a significant fraction of the annual net C emissions from ecosystems such as deciduous forests (Borken et al., 2003), Mediterranean ecosystems (Xu et al., 2004; Placella et al., 2012) and arid/semi-arid ecosystems (Huxman et al., 2004). These types of observations have motivated the incorporation of microbial dormancy into some soil C models (e.g., Blagodatsky and Richter, 1998; Wang et al., 2014; He et al., 2015). These models have modeled dormancy either by estimating the active fraction of the microbial biomass pool (e.g., Blagodatsky and Richter, 1998) or by explicitly simulating transfers between active and dormant biomass pools (e.g., Wang et al., 2014; He et al., 2015). In these models active microbial biomass fraction was assumed to depend on specific external factors such as bioavailable substrate concentration, and typically changed over a time scale of several hours to days. Although predictions of soil C pools and fluxes from these models are strongly dependent on the amounts of active and dormant microbial biomass, the sizes and dynamics of these pools in models have rarely been directly tested against observations of active and dormant microbial biomass. This is likely because the measurements needed to directly test model predictions of active and dormant fractions are scarce. Predictions from models that explicitly represent dormancy are generally tested against observations of total microbial biomass (e.g., Stolpovsky et al., 2011; Wang et al., 2014), R_H (He et al., 2015; Wang et al., 2015), or litter decomposition (Hunt, 1977). Because of the strong link between R_H and the amount of active microbial biomass in soil (Placella et al., 2012; Aanderud et al., 2015; Barnard et al., 2015), it seems reasonable to expect that models that are designed and calibrated to capture fluctuations of active and dormant microbial biomass in soil would be able to predict R_H with higher fidelity than models that do not.

In this study we used a model-data comparison to quantify the implications, in terms of R_H, of including dormancy in a microbial-explicit soil C model. To do this, we measured R_H and active and dormant microbial biomass before, during, and after several rewetting events. We used these data to parameterize an explicit representation of microbial dormancy in an existing microbial-explicit soil C model that has previously been applied at both ecosystem and global scales (Sulman et al., 2014). To our knowledge, this is the first time that a microbial model that explicitly represents dormancy has been calibrated with empirical data of active and dormant microbial biomass in soil. In designing the dormancy model, we attempted to build on previous model implementations in two ways. First, we represented dormancy and activation in a way that integrated the features of the microbial growth environment, including chemical factors such as substrate availability and quality along with physical factors such as soil moisture and temperature. In order to reduce the number of assumptions specific to environmental factors we designed the model to calculate activation and dormancy using potential microbial growth rate rather than functions tied to individual environmental factors such as substrate concentration. Second, to match the rapid changes in active microbial biomass fraction observed in experiments, we designed the model to simulate these changes over time scales of less than 1 h, assuming that active and dormant fractions of microbial biomass adjusted quickly to an equilibrium determined by environmental conditions. To test the generalizability of the relationship between R_H and microbial biomass and activity across soil types, we compared soils from different regions and ecosystems. Because temperature is important for microbial activity in soil (Allison et al., 2010; Salazar-Villegas et al., 2016), we compared soils acclimated to different temperatures. We compared predictions from the dormancy model with predictions from a model using the previous structure in which decomposition is controlled by a single active biomass pool. Because microbial dormancy is virtually ubiquitous in the microbial world (Sussman and Douthit, 1973), transitions between active and dormant state are inherently faster than microbial growth (Blagodatskaya and Kuzyakov, 2013), and active biomass has been shown to be a better predictor of R_H than total microbial biomass (TMB) (Alvarez et al., 1998; Placella et al., 2012; Barnard et al., 2015; Salazar-Villegas et al., 2016), we hypothesized that pulses of R_H immediately following rewetting of dry soils would be better explained by rapid activation of dormant microbes than by net growth (i.e. by fraction of active microbial biomass, FAMB, rather than by TMB), irrespective of soil type and acclimation temperature. Also, because dormancy is a strategy that allows microbes to rapidly respond to adverse environmental conditions (e.g. drought) and survive (i.e. no loss of microbial C biomass), we hypothesized that incorporation of dormancy into the soil C model would lead to reductions in the sensitivity of TMB and (microbially-regulated) R_H to environmental stress.

2. Methods

2.1. Sampling sites and soil collection

We tested our hypotheses using soils from both shrubland and forest, from each of two regions with different mean annual temperature (MAT) and precipitation (MAP): 1) the Coweeta Long Term Ecological Research (LTER) Network site, NC, 35°03′36.0″N 83°25′49.9″W, with MAT 13 °C and MAP 2000 mm; and 2) the Purdue Wildlife Area (shrubland soil), IN, 40°26′45.2″N 87°03′01.8″W, and the Ross Biological Reserve (forest soil), IN, 40°24′45.0″N 87°03′46.7″W,

Table 1
Soil classification and physicochemical properties (USDA, 2017).

Region	Ecosystem	Soil classification	Abbreviation	Slope (%)	pH (0–15 cm)	Bulk density (g cm^{-3})	SOM (%)[a]
NC	Shrubland	Reddies fine sandy loam	ReA	0 to 3	6.4	1.40	6
	Forest	Fannin fine sandy loam	FaD	15 to 30	5.5	1.40	3
IN	Shrubland	Rainsville silt loam	RaB2	2 to 6	6.5	1.45	2
	Forest	Richardville silt loam	RdB2	2 to 6	6.2	1.45	1.5

[a] Soil organic matter (SOM) is expressed as the percentage, by weight, of the soil material with diameter < 2 mm.

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