A theoretical analysis of microbial eco-physiological and diffusion limitations to carbon cycling in drying soils

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ABSTRACT

Soil microbes face highly variable moisture conditions that force them to develop adaptations to tolerate or avoid drought. Drought conditions also limit the supply of vital substrates by inhibiting diffusion in dry conditions. How these biological and physical factors affect carbon (C) cycling in soils is addressed here by means of a novel process-based model. The model accounts for different microbial response strategies, including different modes of osmoregulation, drought avoidance through dormancy, and extra-cellular enzyme production. Diffusion limitations induced by low moisture levels for both extra-cellular enzymes and solutes are also described and coupled to the biological responses. Alternative microbial life-history strategies, each encoded in a set of model parameters, are considered and their effects on C cycling assessed both in the long term (steady state analysis) and in the short term (transient analysis during soil drying and rewetting). Drought resistance achieved by active osmoregulation requiring large C investment is not useful in soils where growth in dry conditions is limited by C supply. In contrast, dormancy followed by rapid reactivation upon rewetting seems to be a better strategy in such conditions. Synthesizing more enzymes may also be advantageous because it causes larger accumulation of depolymerized products during dry periods that can be used upon rewetting. Based on key model parameters, a spectrum of life-history strategies thus emerges, providing a possible classification of microbial responses to drought.

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1. Introduction

The availability of water in soils is highly variable, depending on random rainfall inputs interspaced by dry periods (Rodriguez-Iturbe and Porporato, 2004). This variability affects soil microbes by creating pulses in activity after rainfall, but periods of limited activity when water is unavailable (Austin et al., 2004; Borken and Matzner, 2009). Due to the interactions among microbes, substrates, and water availability, and the timing of rainfall, microbial responses to drought and wetting events are nonlinear. Hence, even small increases in soil moisture after a long dry period may trigger a large respiration pulse. Because these pulsing dynamics may contribute a large fraction of ecosystem respiration (Reichstein et al., 2002; Carbone et al., 2011), including them in process-based models that can effectively predict respiration responses to current and altered hydro-climatic conditions is becoming necessary.

Disentangling physical and biological drivers of respiration pulses and microbial activity is complicated because they are inter-related (Or et al., 2007; Schimel et al., 2007; Moyano et al., 2013). On the one hand, solute diffusivity decreases as the soil becomes drier due to reduced water-filled porosity and increased tortuosity of the water films around solid particles (Skopp et al., 1990; Moldrup et al., 2001). As a result, diffusivity approaches near-zero as soil moisture reaches a point where water films become disconnected. On the other hand, soil matric potentials become more negative, potentially requiring osmotic adjustments for microbial cells to maintain turgor and function (Welsh, 2000; Schimel

et al., 2007). The osmolyte demand, however, might not be met in dry soils due to limited substrate availability (Boot et al., 2013; Kakumanu et al., 2013). In such conditions, switching to a dormant state could be a successful strategy (or the only option), allowing microbes to avoid drought and await moister conditions to resume metabolic activity.

Dormancy may be a useful strategy to maintain a functional and diverse microbial community in the long term (Bär et al., 2002; Jones and Lennon, 2010). However, dormancy may result in delayed recovery of activity upon rewetting (Placella et al., 2012), possibly causing inefficient use of resources that are rapidly made available immediately after a rainfall event. It is also conceivable that extra-cellular enzyme production could be tuned to maximize C uptake (Vetter et al., 1998; Allison, 2012; Moorhead et al., 2012). In drying soils where microbial activity is low, extra-cellular enzymes may still be able to degrade organic matter, causing bioavailable substrates to accumulate, until they become available upon rewetting (Lawrence et al., 2009; Zeglin et al., 2013). Changing the rate and timing of extra-cellular enzyme synthesis could affect these dynamics and certain patterns could maximize the benefits for the microbes.

The presence of this tradeoff between the contrasting needs of surviving drought and being active when resources are available raises the question as to how these strategies (dormancy vs. drought resistance) are coupled with C allocation in microbes (osmoregulation and enzyme synthesis) and ultimately affect soil C storage and respiration pulses. Considering the wide range of microbial responses to drought that has been observed (Freckman, 1986; Lennon et al., 2012), it is conceivable that different microbial communities may employ different strategies depending on the rainfall regime. Here, three eco-physiological modes of response that shape a range of life-history strategies are considered. How each mode functions under varying moisture regimes is evaluated for i) osmoregulation, ii) dormancy/reactivation, and iii) extra-cellular enzyme synthesis. Despite a large degree of flexibility in these strategies, physical limits to acclimation exist (e.g., limited soil and substrate diffusivity) that might constrain the possible range of responses (Manzoni et al., 2012). The question of how these physical processes and physiological responses interact to originate the observed respiration–soil moisture relation has not yet been fully addressed. Here, this question is addressed from a theoretical perspective using a novel process-based soil biogeochemical model that accounts for key physical constraints and physiological responses to drought.

Current soil biogeochemical models employ empirical kinetic rate modifiers to account for soil moisture effects on microbial respiration (Rodrigo et al., 1997; Bauer et al., 2008; Moyano et al., 2012). Typically, these modifiers increase from zero at a lower soil moisture threshold to a unitary value around the soil field capacity or at soil saturation (Manzoni and Porporato, 2007; Lawrence et al., 2009). Other models describe respiration as a function of substrate and oxygen availabilities, which are linked to soil moisture via empirical diffusivity functions (Skopp et al., 1990; Schjonning et al., 2003; Davidson et al., 2012). While accounting in part for diffusion constraints, these models neglect microbial physiological responses to water limitation, and hence cannot capture the mechanistic drivers of the respiration–moisture and soil C–moisture relations.

To provide a description of these processes that captures physiological mechanisms of moisture/drought response, a physiologically-based soil C model accounting for solute diffusion limitations and the dynamics of osmoregulation and dormancy is proposed. Using this model, we first investigate how physiological traits and strategies (osmoregulation, dormancy/reactivation, enzyme production) and physical constraints (diffusivity) control the long-term partitioning of soil C among different pools along moisture gradients. Next, how these biological and physical constraints alter the shape of the respiration–moisture relation and C allocation in microbes during drying and rewetting cycles is assessed.

2. Theory

2.1. Model structure

To focus on the microbial responses to soil moisture variations, soil carbon (C) pools and fluxes only are considered, assuming that nutrients are not limiting. Compartments are expressed as g C m^{-3} of soil and fluxes as g C m^{-3} d^{-1} (full lists of symbols and their units are reported in Tables 1 and 2). The model is to be interpreted at the daily time scale, allowing the elimination of some processes that occur at faster scales. We also focus on the effects of water availability and neglect temperature effects. The proposed model is lumped in space, so that respiration on an area basis (g C m^{-2} d^{-1}) is simply obtained by multiplying the respiration flux by the mean soil depth (Z_r). The model builds on the structure proposed by Schimel and Weintraub (2003), which includes soil organic matter substrates (C_S), soluble organic substrates (C_D), microbial biomass (C_B), and enzyme pools (C_E) (variables and fluxes are defined in Fig. 1). Here, a compartment of dormant biomass ($C_{B,D}$) and two compartments for intra-cellular osmolytes in the active and dormant biomass (C_O and $C_{O,D}$, respectively) are added to improve the description of water stress physiology. We emphasize that

Table 1
List of variables, fluxes, physiological functions, transfer and diffusion coefficients, and other variable quantities. In Fig. 8, subscript T indicates time-integrated quantities over the whole drying period.

Symbol	Description	Units
A/V	Ratio of area around the microbial cells over volume of soil surrounding them	m^{-1}
c	Osmolyte concentration in cytoplasmic free water	mol m^{-3}
C_B	C in active microbial biomass	gC m^{-3}
$C_{B,D}$	C in dormant microbial biomass	gC m^{-3}
C_D	Soluble organic C	gC m^{-3}
C_E	Enzymatic C	gC m^{-3}
C_O	Osmolyte C in active microbial biomass	gC m^{-3}
$C_{O,D}$	Osmolyte C in dormant microbial biomass	gC m^{-3}
C_S	Stable soil organic C substrates	gC m^{-3}
D	Decomposition rate	gC m^{-3} d^{-1}
D_D	Diffusivity of dissolved organic C in bulk soil	m^2 s^{-1}
D_E	Diffusivity of enzymes in bulk soil	m^2 s^{-1}
$f_{A \to D}$	Switching function for active-dormant state transition	—
$f_{D \to A}$	Switching function for dormant-active state transition	—
h_D	Transfer coefficient for dissolved organic C	d^{-1}
h_E	Transfer coefficient for enzymes	d^{-1}
E_P	Enzyme production rate	gC m^{-3} d^{-1}
ET	Evapotranspiration rate	m d^{-1}
I	Rainfall rate	m d^{-1}
I_L	Litterfall rate	gC m^{-3} d^{-1}
M_B	Mortality of active microbial biomass	gC m^{-3} d^{-1}
$M_{B,D}$	Mortality of dormant microbial biomass	gC m^{-3} d^{-1}
$P_{A \to D}$	Transfer from active to dormant population	gC m^{-3} d^{-1}
$P_{D \to A}$	Transfer from dormant to active population	gC m^{-3} d^{-1}
L	Deep percolation rate	m d^{-1}
L_D	Leaching of dissolved organic C	gC m^{-3} d^{-1}
L_E	Leaching of enzymes	gC m^{-3} d^{-1}
R_G	Growth respiration	gC m^{-3} d^{-1}
R_M	Maintenance respiration	gC m^{-3} d^{-1}
U	Microbial uptake	gC m^{-3} d^{-1}
s	Relative volumetric soil moisture	—
φ	Coefficient for increased transition to dormancy under limited C supply	—
Π	Osmolyte allocation	gC m^{-3} d^{-1}
ψ	Soil matric potential	MPa
Ω_B	Osmotic potential of the microbial cell, $\Omega_B = \psi - \pi_B$	MPa