



Adaptation of microbial resource allocation affects modelled long term soil organic matter and nutrient cycling



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ABSTRACT

In order to understand the coupling of carbon (C) and nitrogen (N) cycles, it is necessary to understand C and N-use efficiencies of microbial soil organic matter (SOM) decomposition. While important controls of those efficiencies by microbial community adaptations have been shown at the scale of a soil pore, an abstract simplified representation of community adaptations is needed at ecosystem scale.

Therefore we developed the soil enzyme allocation model (SEAM), which takes a holistic, partly optimality based approach to describe C and N dynamics at the spatial scale of an ecosystem and time-scales of years and longer. We explicitly modelled community adaptation strategies of resource allocation to extracellular enzymes and enzyme limitations on SOM decomposition. Using SEAM, we explored whether alternative strategy-hypotheses can have strong effects on SOM and inorganic N cycling.

Results from prototypical simulations and a calibration to observations of an intensive pasture site showed that the so-called revenue enzyme allocation strategy was most viable. This strategy accounts for microbial adaptations to both, stoichiometry and amount of different SOM resources, and supported the largest microbial biomass under a wide range of conditions. Predictions of the holistic SEAM model were qualitatively similar to predictions of the SYMPHONY model, which explicitly represents competing microbial guilds. With adaptive enzyme allocation under conditions of high C/N ratio of litter inputs, N that was formerly locked in slowly degrading SOM pools was made accessible, whereas with high N inputs, N was sequestered in SOM and protected from leaching.

The findings imply that it is important for ecosystem scale models to account for adaptation of C and N use efficiencies in order to represent C-N couplings. The combination of stoichiometry and optimality principles is a promising route to yield simple formulations of such adaptations at community level suitable for incorporation into land surface models.

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1. Introduction

The global element cycles of carbon (C) and nitrogen (N) are strongly linked and cannot be understood without their intricate interactions (Thornton et al., 2007; Janssens et al., 2010; Zaehle and Dalmonech, 2011). The ties between nutrient cycles are especially strong in the dynamics of soil organic matter (SOM), because the depolymerisation and mineralisation of SOM relies on a microbial decomposer community with a rather strict homeostatic regulation of their stoichiometry, i.e. their elemental ratio of C/N (Sturner and

Elser, 2002; Zechmeister-Boltenstern et al., 2015). Therefore, it is important to represent effects of microbial control on soil biogeochemistry also in ecosystem to global scale models (Todd-Brown et al., 2012; Xu et al., 2014).

C and N fluxes controlled by microbial stoichiometry comprise respiration of organic C, mineralization of organic N, and immobilization of inorganic N. They occur if decomposers experience stoichiometric imbalance, i.e. differences in elemental composition between food and the requirement of feeders (Sturner and Elser, 2002). Decomposers require a certain amount of C for each unit of N. With balanced growth, i.e. when stoichiometry of the food matches the requirements, decomposers can utilize all food for productive purposes such as synthesis of new biomass or enzymes, growth respiration, and maintenance respiration. If there is

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different amount of C per unit N in the food, decomposers have to deal with this imbalance in some way.

Decomposers can - in principle - adjust in three different ways when faced with imbalances between the stoichiometry of the organic material (OM), i.e. the litter and SOM they feed on, and their own stoichiometric requirements (Mooshammer et al., 2014b). First, individual microbes can adapt their carbon-use efficiency (CUE), or their nutrient-use efficiency (Sinsabaugh et al., 2013). The alteration of CUE has shown to have large consequences on prediction of carbon sequestration in SOM (Allison, 2014; Wieder et al., 2013). Regulation of nutrient use efficiency has consequences for nutrient recycling and loss of nutrients from the ecosystem (Mooshammer et al., 2014a) and soil plant feedback (Rastetter, 2011). Second, decomposer communities can adapt their stoichiometric requirements. Community composition can shift between species with high C/N ratio, such as many fungi, or species with lower C/N ratio, such as many bacteria (Cleveland and Liptzin, 2007; Xu et al., 2013), although the flexibility is relatively narrow. Third, decomposers can adapt their allocation of resources into synthesis of different extracellular enzymes to preferentially degrade fractions of SOM that differ by their stoichiometry (Moorhead et al., 2012).

Representation and consequences of stoichiometry on element cycling differ between models at different scales. Most models at ecosystem scale employ the first decomposer imbalance option, and use changes in CUE or nutrient use efficiency to represent stoichiometric controls on respiration and mineralization fluxes (Manzoni et al., 2008). However, modelling studies at the pore scale have demonstrated the important effect of community adaptation and their emerging effects on element cycling (Allison and Vitousek, 2005; Resat et al., 2011; Wang et al., 2013). Explicit representation of competition among several microbial groups that differ in their expression of different enzymes resulted in a comparable simulated CUE across a wide range of litter stoichiometry (Kaiser et al., 2014). Likely, therefore, there is a need to capture the effects of community adaptation also in models at ecosystem scale.

At least two alternatives exist to represent the effects of microbial diversity at the ecosystem scale. First, competition of several microbial populations can be explicitly modelled to represent stoichiometric effects such as sustained sequestration of N with high N inputs (Perveen et al., 2014). Second, adaptation of effective properties of the entire microbial community, such as investments into nutrient uptake (Rastetter et al., 1997; Rastetter, 2011) can represent the emerging effects in an abstract, but dynamic and adaptive way. The adaptation of enzyme allocation was recently formalised using the second imbalance strategy by the conceptual EEZY model (Moorhead et al., 2012) and further developed using the EnzMax allocation strategy by Averill (2014). While these models show strong strategy effects on nutrient cycling at a time scale of days to months, they do not represent feedback mechanisms to the size and stoichiometry of the SOM pools, and therefore they cannot study the consequences for decadal SOM dynamics.

In this paper, we adopt the second alternative of representing microbial diversity as working hypothesis and propose a holistic scheme to represent effects of microbial adaptation of enzyme synthesis on SOM cycle at the ecosystem scale. Our aim was to tackle the need of capturing the decadal time scale effects of adaptive enzyme synthesis on SOM dynamics and nutrient recycling. We therefore extended the EEZY model to explore different consequences of alternative enzyme allocation strategies.

This paper first introduces the SEAM model (Section 2.1), a dynamical model of SOM cycling that explicitly represents microbial strategies of producing several extracellular enzyme pools (Section 2.3). Next, the effects of those strategies on SOM cycling are presented by prototypical examples (Sections 2.4 and 3.1).

Finally, a calibration to an intensive pasture site (Section 2.5) demonstrates the usability of the model (Section 3.2) and compares its predictions to the ones of the SYMPHONY model (Perveen et al., 2014), which explicitly models several microbial-groups.

2. Methods

2.1. Soil Enzyme Allocation Model (SEAM)

The dynamic Soil Enzyme Allocation Model (SEAM) allows exploring consequences of enzyme allocation strategies for SOM cycling at the soil core to ecosystem scale from monthly to decadal scale. The modelled system are C and N pools in SOM in a volume of soil. The system could be soil of a laboratory incubation or a layer of a soil profile, e.g. its upper 20 cm. The model represents different SOM pools containing C and N as state variables and specifies differential equations for the mass fluxes. It is driven by C and N inputs of plant litter (both above-ground and rhizodeposition), inorganic N inputs from deposition and fertilisers, as well as prescribed uptake of inorganic N by roots. SEAM computes output fluxes of heterotrophic respiration and leaching of inorganic N.

Key features are: first, the representation of several SOM pools that differ by their stoichiometry, and second, the representation of enzymes that degrade specifically those SOM pools. The quality spectrum is modelled by two classes: a C rich litter pool, L, and a N rich pool that consists of microbial residues, R (Fig. 1, Table 1). The most important assumptions are described in the following paragraphs, while the symbols are explained in Table A.5 and detailed model equations are provided with Appendix A.

Decomposition of the litter and residue pools follows reverse Michaelis-Menten kinetics (Schimel and Weintraub, 2003), which is first-order to the amount of OM, and saturates with the amount of the respective enzyme. C/N ratios, β , of the decomposition flux are equal to the C/N ratios of the decomposed pool. The C/N ratios of biomass and enzymes are assumed to be fixed, while those of the substrate pools may change over time due to changing C/N ratio of total influxes to these pools. Imbalances in stoichiometry of uptake and microbial requirements are compensated by overflow respiration or N mineralization. This means that if there is more C in

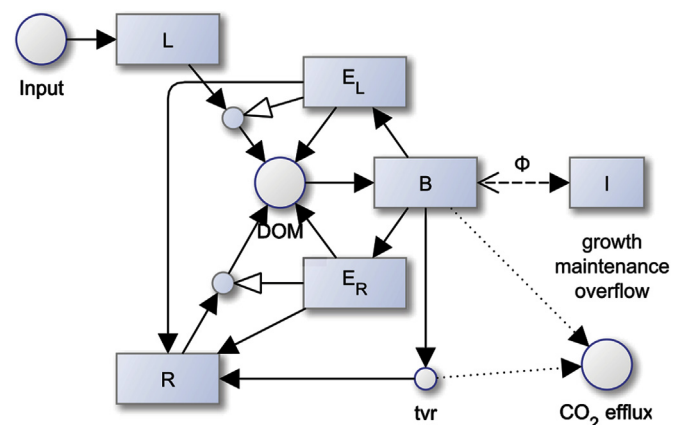


Fig. 1. Model structure of SEAM: Two substrate pools (L and R) which differ in their elemental ratios are depolymerized by respective enzymes (E_L and E_R). The simple organic compounds (DOM) are taken up by the microbial community and used for synthesizing new biomass (B), new enzymes, or for catabolic respiration. Turnover of microbial biomass (tvr) is in part mineralized and the rests adds to the residue pool. Stoichiometric imbalance between DOM and B causes overflow respiration or mineralization/immobilization (Φ_B) of inorganic N (I) (further detailed in Fig. 2). Boxes correspond to pools, disks to fluxes, black arrow heads to mass fluxes, white arrow heads to other controls. Solid lines represent fluxes of both C and N, while dotted and dashed lines represent separate C or N fluxes respectively.

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