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Soil organic matter decomposition driven by microbial growth: A simple model for a complex network of interactions

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Abstract

Priming effects are expressions of complex interactions within soil microbial communities. Thus, we aimed at building a microbial population growth model which could deal with different substrates, resources and populations. Our model divides the decomposition/growth process at the population level in two stages, mimicking mechanisms taking place at molecular and cellular scales: (1) the first stage is a reversible process whereby microbial biomass capture their substrate to form a complex within definite proportions; (2) the second stage is the irreversible rate-limiting utilization of substrate per se. It is supposed to be a first order process with respect to the quantity of complex. We put these assumptions into equations using an analogy with chemical reactions at equilibrium. We show that this model (1) provides a mathematical formalism that bridges the gap between first order decay of substrates and Monod kinetics; (2) sets constraints on the possible combinations of microbial functional traits, yielding microbial strategies in agreement with observations; (3) allows to model both positive and negative priming effects, and more generally complex interactions between the various components of a soil system. This model is designed to be used as a kernel in any soil organic matter model.

Keywords: Monod kinetics; First order kinetics; Stoichiometry; Colimitation; Multiple limitation; Maintenance; Priming effects

1. Introduction

First order kinetics have long been the mainstay in soil organic matter models (McGill, 1996) because they are often good approximations of mass losses in litter bags. However, litter decomposition takes place in soils where, through microbial action, it is liable to interact with native soil organic matter decomposition. These interactions have been recently experimentally demonstrated using isotope tracing (for instance Wu et al., 1993; Fontaine et al., 2004b). In unlabeled soils, any change in unlabeled CO_2 respiration after the addition of a labeled substrate has been termed a priming effect (Kuzyakov et al., 2000). There is an increasing number a studies which suggest that priming effects are ubiquitous, can be of quantitative importance (Kuzyakov et al., 2000; Fontaine et al., 2004a; Hamer and Marschner, 2005) and are very variable in intensity and in direction (positive or negative, see also Hamer and Marschner, 2002). It seems that priming effects cannot be accounted for with linear effects and even that their interpretation may need to take into account antagonistic effects specific of different microbial functional groups (Bell et al., 2003; Fontaine et al., 2003; 2004b; Hamer and Marschner, 2005).

Priming effects are perhaps the most conspicuous reason why one should want to see soil organic matter models based on a more mechanistic, microbially-driven treatment of decomposition, as already advocated by McGill (1996). But, because decomposition is driven by microbial growth, features such as microbial stoichiometric and maintenance requirements also have important consequences on soil organic matter dynamics. Recent models have introduced a number of microbial constraints (Gignoux et al., 2001; Schimel and Weintraub, 2003), but these attempts were not without parameterization troubles, especially for maintenance rates (Gignoux et al., 2001). Actually, it turns out that it is not so easy to introduce microbial growth as modeled by microbiologists in soil organic matter models.

First, just as first order kinetics have been the mainstay in soil organic matter models, Monod model has been

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the mainstay in microbiology (Kovarova-kovar and Egli, 1998). Unfortunately, these two models are incompatible with each other's hidden assumptions. Monod model assumes that the microbial specific growth rate is ultimately limited, whereas the first order decay rate of the substrate is not. Indeed, writing that a biomass increment follows a Monod curve: $db/dt = \mu b(s/K + s)$ means that the first order substrate consumption rate $(1/s)(ds/dt)$ can increase infinitely as biomass increases. First order kinetics with respect to the substrate yield just the opposite: if the substrate concentration is increased, the biomass could potentially grow infinitely fast. Therefore, these two models seem to be totally different in essence. Second, later microbial growth models in microbiology have mainly focused on detailed intracellular processes (Koch, 1997; Kovarova-kovar and Egli, 1998), and as such are not suitable for soil modeling. Third, most microbial growth models have been designed for suspended cultures growing on soluble substrates, whereas, in soils, insoluble substrates are predominant and might lead to different behaviors.

Therefore, the aim of this work was to build a model at the population or at the community level able to reconcile the microbiologists' insights with the soil organic matter decomposition process. It is not a soil organic matter model in itself, but is intended to be used as a microbial growth based kernel in any soil organic matter model. For that purpose, we kept it as simple as possible. It is based on a two-stage formulation of decomposition/growth, leading to two key assumptions regarding these stages. We give three qualitative applications of the model that makes it a potentially useful model. First, we show that the model does bridge the gap between first order decay and Monod kinetics. Second, we show that the model yields predictions about microbial physiology consistent with experimental evidence: this may help to refine microbial strategies. Finally, we show that the two simple assumptions of the model make complex interactions between substrates and microbial populations possible. In particular, we illustrate the ability of the model to predict positive as well as negative priming effects.

2. Model description

2.1. One population, one substrate

Notations of variables and parameters are listed in Table 1. We will first consider one microbial population B and a single substrate S. We will denote abundances by small letters. We will express abundances in units of moles of carbon per kg of soil (C-moles). The model assumes that decomposition is driven by microbial growth, therefore:

$$-\frac{ds}{dt} \propto \frac{db}{dt}$$

The model splits the decomposition/growth process into two stages. The first one is a stage where microbial biomass must capture enough resources before subsequent processing. When microbes have collected a piece of substrate, we will say that they form a complex together. The second stage is the subsequent utilization of complexed substrate to yield new biomass.

Table 1
Summary of the model parameters and variables

Symbol	Meaning
B	Microbial biomass concentration
S	Substrate concentration
X	Complex formed by biomass and substrate
ν	Stoichiometric coefficient of the substrate in the complex
μ	First order constant of stage 2 in the model
η	Carbon to nitrogen ratio of microbial biomass (mole basis)
Y_c	Carbon yield: number of units of b formed per mole of carbon uptaken
Y_{cmax}	Growth carbon yield: carbon yield if maintenance is set to zero
Y_n	Nitrogen yield: number of moles of nitrogen required to form one unit of biomass
G	Instantaneous specific growth rate of microbes on a given substrate
D	Instantaneous specific decay rate of substrate by a given microbial population
μ_{max}	Maximum specific growth rate of microbes
k_{max}	Maximum first order decay rate of substrate
K	Affinity of a given microbial population for a given substrate
m_t	Turnover rate coefficient of biomass
m_x	Maintenance energy coefficient of biomass

Specifically, the model is based on two hypotheses.

Hypothesis 1. The first stage is reversible and each unit of biomass must capture a definite number of units of substrate before entering stage 2. This definite number, denoted by the stoichiometric coefficient ν, sets when resources are in sufficient amount for being processed through stage 2. At any time, we note x the quantity of biomass which has formed a complex with a quantity νx of substrate. We will call x the complexed fraction of biomass and $b-x$ the free fraction. Likewise, νx will be called the complexed fraction of substrate and $s-\nu x$ its free fraction.

Hypothesis 2. The second stage is irreversible and rate-limiting of the whole process. It is a first order process with respect to x, and its first order constant will be denoted by μ.

Concretely speaking, substrates are either soluble or insoluble. The solubilization step is generally the irreversible, rate-limiting step of decomposition and growth on insoluble substrates (Lynd et al., 2002). Then, complexing an insoluble substrate simply means that microbial cells will get adsorbed on or attached to their substrate, such as bacteria on cellulose. Detachment may occur so that it is a reversible process. In contrast, for a soluble substrate which can be readily uptaken inside the cell, capturing it is presumably equivalent to absorbing it into the cell. Excretion of the substrate as is or as slightly transformed metabolites is the opposite process. This mechanism is known to happen and is called 'overflow metabolism' (Russell and Cook, 1995). The irreversible, rate-limiting