

Soil Biology & Biochemistry 40 (2008) 1137–1148

Soil Biology & **Biochemistry** 

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# Soil heterogeneity in lumped mineralization–immobilization models

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Received 31 May 2007; received in revised form 30 November 2007; accepted 4 December 2007 Available online 14 January 2008

### Abstract

The heterogeneous distribution of nutrient-rich and nutrient-poor patches in soils strongly affects the intensity of nitrogen cycling between organic and inorganic soil compartments. In highly heterogeneous soils, observation at the core scale of large gross mineralization and immobilization fluxes has led to the development of the mineralization–immobilization turnover (MIT) modeling scheme, which maintains that all nitrogen decomposed from organic compounds is mineralized before assimilation by the microbial biomass. This hypothesis, however, neglects the endogenous nature of the ammonification reactions at the microscopic scale, where organic N is directly assimilated by the decomposers and only the surplus is released as ammonium, as better described by the direct (DIR) pathway. Here we hypothesize that, at the micro-scale, mineralization behaves according to the DIR pathway and analyze a simple two-compartment model to simulate a heterogeneous soil with two fractions of different chemical composition (i.e., C-to-N ratio) and quality (i.e., decomposition rate). We derive the effective parameters of the aggregated model as a function of micro-scale features, and show that it represents a generalization of the parallel (PAR) scheme, which in its original form was introduced to combine DIR and MIT pathways. This physically based new parameterization improves current lumped N mineralization models.  $\odot$  2007 Elsevier Ltd. All rights reserved.

Keywords: Bio-geochemical models; Soil heterogeneity; Mineralization; Immobilization; Nitrogen limitation; Variable aggregation

### 1. Introduction

Soils are spatially heterogeneous at molecular to landscape scales [\(Kandeler et al., 2001](#page--1-0); [Ettema and Wardle,](#page--1-0) [2002](#page--1-0)). The spatial variability of physical properties couples with chemical heterogeneity of soil organic matter (SOM) ([Haynes and Swift, 1990\)](#page--1-0) resulting in a variety of microhabitats ([Young et al., 1998](#page--1-0)). As a consequence, well-defined patterns of soil biological activity emerge at the  $\mu$ m-to-mm scales, where microbial growth is concentrated in rich microsites in the rhizosphere or around decaying roots, and at cmto-m scale, possibly due to macro-porosity and preferential flow paths [\(Nunan et al., 2002](#page--1-0)). The presence of micro-sites of contrasting nutrient availability may result in intense nitrogen (N) cycling between nutrient-rich sites mineralizing nitrogen and relatively nutrient-poor ones immobilizing it ([Schimel and Bennett, 2004\)](#page--1-0).

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Evidence of the role of heterogeneous distribution of nutrients is supported by the observation of recycling of soil N at the core scale (e.g.,  $\approx 10 \text{ cm}^3$ ), which may be interpreted as the macroscopic result of micro-scale dynamics. At the macroscopic level, the decomposed organic N appears to be only partially assimilated by microbes, while the rest is transferred into the mineral N pool, where it can then be immobilized ([Saetre and Stark,](#page--1-0) [2005](#page--1-0); [Bruun et al., 2006](#page--1-0)). The mathematical representation of this macroscopic scenario has been referred to as the parallel (PAR) hypothesis [\(Barraclough, 1997](#page--1-0); [Manzoni](#page--1-0) [and Porporato, 2007\)](#page--1-0). At the micro-scale, this partial assimilation does not seem realistic, as organic N from decomposition must be assimilated by the microbial cells for deamination to occur. When the cell demand for N is satisfied, ammonium is released [\(Barak et al., 1990](#page--1-0); [Haynes](#page--1-0) [and Swift, 1990](#page--1-0)); on the contrary, when organic N sources are scarce, microbes tend to immobilize N from the inorganic compartment. Hence, it has been suggested that recycling patterns are controlled by different microbial

<sup>0038-0717/\$ -</sup> see front matter  $\odot$  2007 Elsevier Ltd. All rights reserved. doi:[10.1016/j.soilbio.2007.12.006](dx.doi.org/10.1016/j.soilbio.2007.12.006)

communities in relatively N-rich and N-poor micro-sites, respectively, mineralizing and consuming nitrogen [\(Schimel](#page--1-0) [and Bennett, 2004;](#page--1-0) [Schimel and Hattenschwiler, 2007\)](#page--1-0). This macroscopic behavior has been previously related to soil heterogeneity ([Davidson et al., 1990](#page--1-0); [Drury et al.,](#page--1-0) [1991\)](#page--1-0), but has not been justified theoretically.

While most bio-geochemical models are based on chemically different compartments (e.g., [Parton et al.,](#page--1-0) [1987;](#page--1-0) [Porporato et al., 2003\)](#page--1-0), few actually parameterize the effects of the heterogeneous placement of residues in the soil [\(Breland, 1997;](#page--1-0) [Magid et al., 2006](#page--1-0)), or explicitly account for spatial heterogeneity [\(Korsaeth et al., 2001](#page--1-0); [Allison, 2005](#page--1-0); [Ginovart et al., 2005](#page--1-0)). In this work, we develop a simple conceptual model of C and N cycling in a heterogeneous soil. We consider two compartments, each describing a class of micro-sites with contrasting chemical composition, but sharing a pool of mobile inorganic N. Assuming realistic kinetic laws for C and N metabolism at the micro-site level (e.g., direct assimilation of organic N), we aggregate the C and N fluxes of the single soil fractions into an equivalent lumped model. We show that the resulting scheme is a generalization of PAR hypothesis and that the observed patterns of mineralization and immobilization can be explained by the distribution of N-rich and N-poor substrates. We also investigate how the nonlinear character of the microbial–substrate coupling affects the aggregated equations.

### 2. Model development and results

We refer to Fig. 1 for a schematic representation of the chemically heterogeneous soil system (Fig. 1a) and its equivalent homogeneous one (Fig. 1b), while the used symbols are described in [Table A1](#page--1-0). The heterogeneous soil is assumed to be formed by two active fractions, lumped in space, but characterized by different C/N ratios and chemical properties. Each fraction is used as a conceptualization of functionally different micro-sites that exchange matter (e.g., nitrogen) according to stoichiometric laws. For example, the first fraction may represent fresh decomposing litter that has been mixed into a less active organic soil matrix or with a litter of different N status (the second fraction), as in the microcosms devised by [Schimel and Hattenschwiler \(2007\).](#page--1-0)

## 2.1. Modeling framework

We describe only instantaneous fluxes of decomposed substrate,  $C_s$ , through the microbial biomass,  $C_B$ , assuming a certain distribution of C and N concentrations in the



Fig. 1. Simplified schemes of carbon and nitrogen cycling through the microbial biomass: fluxes and pools in the heterogeneous (a) and the homogeneous soil (b). White compartments and dashed lines represent N pools and fluxes; shaded compartments and continuous lines refer to the corresponding C pools and fluxes. Net mineralization (or net immobilization) in (b)  $(Eq. (7))$  is indicated with a dot-dashed line to distinguish it from the internal N recycling  $(1 - \eta) \text{DEC}(C/N)^{-1}$ . The net nitrogen flux exchanged between microbial biomass and mineral N in (b) is denoted by  $\Phi$  (Eq. (18)).

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