Soil Biology & Biochemistry 42 (2010) 1212–1221

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Comparing two mechanistic formalisms for soil organic matter dynamics: A test with in vitro priming effect observations

Cathy Neill*, Bertrand Guenet

Université Pierre et Marie Curie, Laboratoire Biogéochimie et Ecologie des Milieux Continentaux, UMR 7618 CNRS/Paris 6, 46 rue d'Ulm, 75230 Paris Cedex 05, France

ARTICLE INFO

Article history:
Received 29 January 2010
Received in revised form
16 April 2010
Accepted 21 April 2010
Available online 7 May 2010

Keywords:
Model comparison
Maximum caliber
Organic matter dynamics
Litter decomposition
Mineral nitrogen
Microbial biomass
^{13}C labelling
Priming effect

ABSTRACT

First order kinetics characterize most models of soil organic matter dynamics. Although first order kinetics often provide a good description of litter decomposition, their general applicability has recently been challenged by numerous observations of priming effects. A priming effect can be defined as a change in native soil organic matter decomposition rate following the addition of some labelled exogenous substrate. Recently two new formalisms were developed which predict a priori the existence of priming effects, whether positive or negative. The Extended Mass Action (EMA) formalism is a generalization of enzyme kinetics at the microbial scale. The Maximum Caliber (MAXCAL) formalism describes the most probable dynamics of a system that arises when the multiple ways feasible macroscopic dynamics can be realized at the microscopic particle scale are accounted for. Here those two formalisms were applied to a common soil compartimentation scheme and their predictions confronted with an appropriate set of priming observations. We show that the two formalisms generate distinct, testable predictions and that the MAXCAL formalism performed better than the EMA formalism. We discuss the determinants of priming effects as predicted by the Maximum Caliber formalism.

1. Introduction

Soil organic matter performs a number of key functions in agroecosystems. It is a major reservoir of nutrients for plants. It also maintains an aggregated soil structure enabling water and air movement in soils. On a global scale, soil carbon is an important pool as well. It is a quantitatively important pool (approx. twice the atmospheric carbon pool (Schlesinger and Andrews, 2000)), and has proven sensitive enough to global changes to represent either a significant carbon sink or source (Guo and Gifford, 2002; Paul et al., 1997; Lal et al., 1995).

Our current understanding of soil organic matter dynamics is synthesized and quantitative predictions made possible with the help of mathematical models. Soil organic matter models are numerous (reviewed in Manzoni and Porporato, 2009). They usually differ in the way they partition soil organic matter into compartments (or "fractions"). However, many of them, including the popular Century model (Parton et al., 1987), share a common mathematical formalism, namely first order kinetics.

First order kinetics assume that the decomposition rate of some organic fraction is proportional to the amount of carbon in that fraction (although some nitrogen limitation may be included based on microbial stoichiometric requirements for N).

Despite the consensus on the robustness of these kinetics reflected by current models, first order kinetics are questionable. They indeed fail to account for organic matter dynamics as observed with isotope labelling and tracing. Short to medium-term incubations of soil samples amended with ^{14}C or ^{13}C labelled substrates have consistently shown that decomposition processes of distinct substrates interact with one another (reviewed in Blagodatskaya and Kuzyakov, 2008; Kuzyakov et al., 2000). Adding some labelled substrate may suppress or enhance native (unlabelled) soil organic matter mineralization. This phenomenon, known as the priming effect – whether positive or negative – seemingly contradicts first order kinetics. Indeed first order kinetics entail no interactions between the decomposition processes of distinct substrates.

As priming effects may be quantitatively important at the yearly scale and perhaps even more so if their cumulative effects are considered on the long run (e.g. Fontaine et al., 2004a, 2007), the following questions arise: How can we model them? What would

* Corresponding author at: Present address: Bioemco, Centre INRA Versailles-Grignon, Bâtiment Eger, 78850 Thiverval-Grignon, France. Tel.: +33 1 30 81 59 58; fax: +33 1 30 81 54 97.
E-mail addresses: neill@biologie.ens.fr (C. Neill), guenet@biologie.ens.fr (B. Guenet).

0038-0717/$ – see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.soilbio.2010.04.016

be the consequences for long-term kinetics? Should we change our current modelling consensus about first order kinetics?

Recently Neill and colleagues developed a new modelling approach to ecosystem dynamics (Neill and Gignoux, 2008; Neill et al., 2009). This approach is applicable to soil systems as well. It is a combinatorial approach that consists in calculating the trajectory of a system that is most probable because it can be realized in more ways at the individual "particle" scale (whether particles of matter or living particles). The number of ways a trajectory can be realized at a microscopic scale has been coined the "caliber" by Jaynes (1985). The model predicts that a system will follow its maximum caliber trajectory.

When applied to a soil system consisting of labelled and unlabelled organic fractions, and one explicit microbial pool, the maximum caliber ("MAXCAL") formalism predicts a priori the existence of positive and negative priming effects as the result of two antagonistic mechanisms: on the one hand, native soil organic matter mineralization is an increasing function of microbial biomass, which may increase if fed by the added substrate; on the other hand, native soil organic matter mineralization is a decreasing function of the availability of other substrates, because substrates compete with one another to be decomposed by microbes. If microbes have a higher affinity for the added substrate, they will utilize it preferentially and this may induce a negative priming effect.

An alternate formalism that can produce positive and negative priming effects has been offered by Neill and Gignoux (2006). This formalism can be derived from an analogy between decomposition processes and enzymatic reactions, using the law of mass action. Neill and Gignoux (2006) showed that it generalizes well-known formalisms such as the Michaelis–Menten formalism, its inverse, or the Beddington-DeAngelis formalism (Beddington, 1975; DeAngelis et al., 1975). We will call it the "extended mass action" formalism, "EMA" in short.

The two formalisms, MAXCAL and EMA, are in fact intriguingly similar, but they do differ in some important aspects, and are derived from entirely different rationales. It seemed interesting to compare them and rate them with quantitative data on priming effects. To do so, we used a series of incubations of cultivated soils amended with various amounts of ^{13}C labelled wheat straw and mineral nitrogen (Guenet et al., submitted). This paper reports the results of this model comparison.

2. Model description and methods

2.1. The data

To test the two formalisms, we used a series of 80 day in vitro soil incubations that are described and discussed in detail elsewhere (Guenet et al., submitted). Briefly, the soil used was a cultivated soil from Paris area, France (C:N ratio of 10, 10.4 g C/kg soil). 20 g soil samples were incubated at constant temperature (20 °C) and humidity (pF 2.75) in 120 mL flasks. The experiment followed a 4 × 3 incomplete factorial design, the first factor being the addition of ^{13}C labelled wheat straw (C:N ratio of 44) and the second factor the final C:N ratio of exogenous inputs (the latter being manipulated by additions of mineral nitrogen), yielding a total of nine treatments plus one control. Table 1 sums up the various amounts added. For instance treatment C1N1 corresponded to an addition of 1.5 g C straw per kg soil and 16 mg mineral nitrogen, which, including the nitrogen content of the straw, yielded a final input C:N ratio of 30. ^{13}C labelled and unlabelled CO_2 respiration were measured throughout the incubation period. In all, 15 replicates per treatment were set up, permitting the destructive harvest of three of the replicates on incubation days 3, 7, 15, 28 and 80 for mineral nitrogen concentration measurements. Figs. 1, 2 and 3 show the dynamics of cumulated labelled and unlabelled CO_2 and mineral nitrogen concentration respectively.

Table 1
Experimental treatments.

Treatment Name	Straw added (gC kg^{-1} soil)	Mineral nitrogen added (gN kg^{-1} soil)	Final input C:N ratio
Control C0N0	0	0	n.a.
C1N0	1.5	0	44
C2N0	2.2	0	44
C3N0	3.2	0	44
C1N1	1.5	0.016	30
C2N1	2.2	0.0235	30
C3N1	3.2	0.0346	30
C1N2	1.5	0.0395	20
C2N2	2.2	0.0581	20
C3N2	3.2	0.0854	20

2.2. The model structure

The comparison of the two formalisms required a common model structure upon which both formalisms could be applied. We chose the simplest model structure to represent the incubated soils, namely one native, unlabelled soil organic matter pool (hereafter denoted humus because soil was collected at depth >5 cm and sieved to remove most fresh plant residues), one ^{13}C labelled wheat straw pool (denoted litter), one microbial pool and one mineral nitrogen pool (Fig. 4). This parsimonious choice had advantages and drawbacks. On the one hand, successful predictions stemming from a simple model structure gives more credit to the mathematical formalism applied upon that structure, whereas positive results obtained with an over-parameterized model are difficult to interpret. On the other hand, an overly simple model structure can jeopardize the ability of the formalism to account for the data. We will return to this issue below.

With this model structure, we assumed three microbial fluxes would govern the dynamics of the whole system: microbial growth on humus, x_h, microbial growth on litter, x_l, and microbial mortality z. We assumed those three fluxes would determine all the other fluxes through stoichiometric relationships (Fig. 4), so that the dynamics of the system could be described by the following equations:

$$\delta c_h = -\nu_h x_h + \eta z \quad (1)$$

$$\delta c_l = -\nu_l x_l \quad (2)$$

$$\delta b = x_h + x_l - z \quad (3)$$

$$\delta n = (n_h \nu_h - n_b) x_h + (n_b - \eta n_h) z - (n_b - n_l \nu_l) x_l \quad (4)$$

where c_h, c_l, b and n stand for humus carbon, litter carbon, microbial biomass carbon and mineral nitrogen respectively and the symbol δ denotes their variation over a small time step δt (Table 2 sums up the model parameters and state variables). Units chosen for c_h, c_l and b were gC per kg of soil, and gN per kg of soil for n. Eq. (1) says that for any new microbial unit grown on humus, ν_h humus units have been decomposed (and thus $\nu_h - 1$ units have been mineralized to CO_2). Likewise ν_l denotes the number of litter units needed to make up one new microbial unit. When c_h, c_l and b are expressed in gC per kg soil, ν_h and ν_l can be viewed as inverse of carbon assimilation yields. Next, for any microbial unit that dies, a fraction η of it is humified and thus feeds the humus stock. The rest is mineralized to CO_2, accounting in particular for maintenance respiration.