

Model of apparent and real priming effects: Linking microbial activity with soil organic matter decomposition

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ARTICLE INFO

Article history:

Received 8 November 2009

Received in revised form

6 April 2010

Accepted 7 April 2010

Available online 20 April 2010

Keywords:

Modeling of decomposition

Carbon turnover

Microbial biomass activity

Apparent and real priming effects

Soil organic matter turnover

¹⁴C

ABSTRACT

The most frequently used models simulating soil organic matter (SOM) dynamics are based on first-order kinetics. These models fail to describe and predict such interactions as priming effects (PEs), which are short-term changes in SOM decomposition induced by easily available C or N sources. We hypothesized that if decomposition rate depends not only on size of the SOM pool, but also on microbial biomass and its activity, then PE can be simulated. A simple model that included these interactions and that consisted of three C pools – SOM, microbial biomass, and easily available C – was developed. The model was parameterized and evaluated using results of ¹²C–CO₂ and ¹⁴C–CO₂ efflux after adding ¹⁴C-labeled glucose to a loamy Haplic Luvisol. Experimentally measured PE, i.e., changes in SOM decomposition induced by glucose, was compared with simulated PE. The best agreement between measured and simulated CO₂ efflux was achieved by considering both the total amount of microbial biomass and its activity. Because it separately described microbial turnover and SOM decomposition, the model successfully simulated apparent and real PE.

The proposed PE model was compared with three alternative approaches with similar complexity but lacking interactions between the pools and neglecting the activity of microbial biomass. The comparison showed that proposed new model best described typical PE dynamics in which the first peak of apparent PE lasted for 1 day and the subsequent real PE gradually increased during 60 days. This sequential decomposition scheme of the new model, with immediate microbial consumption only of soluble substrate, was superior to the parallel decomposition scheme with simultaneous microbial consumption of two substrates with different decomposability. Incorporating microbial activity function in the model improved the fit of simulation results with experimental data, by providing the flexibility necessary to properly describe PE dynamics. We conclude that microbial biomass should be considered in models of C and N dynamics in soil not only as a pool but also as an active driver of C and N turnover.

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1. Introduction

Predicting the consequences of climate change on ecosystem carbon (C) fluxes and their feedbacks depends on understanding the co-limitation of the decomposition of soil organic matter (SOM) by the quantity and quality of available substrate and by the activity of decomposers (Fang et al., 2005; Wutzler and Reichstein, 2008). SOM turnover models based on first-order kinetics that do not consider such co-limitation fail to describe so-called priming effects (PEs). According to Kuzyakov et al. (2000), PEs are strong (up to 10-fold larger than in control soil) and generally short-term

(up to several months) changes in the turnover of native soil organic matter induced by comparatively moderate treatments of the soil. Such treatments might be inputs of organic or mineral fertilizer to the soil (Jenkinson et al., 1985; Olayinka, 2001; Leifeld et al., 2002; Bol et al., 2003; Fanguelro et al., 2007), exudation of organic substances by roots (Paterson, 2003; Cheng and Kuzyakov, 2005; Cheng, 2009), or inputs of plant residues (Bell et al., 2003; Perelo and Munch, 2005). In the course of priming, large amounts of C, N, and other nutrients can be released in soil very quickly, generally over several days to weeks (Fu et al., 2000; Hamer and Marschner, 2002, 2005; Bol et al., 2003; Fontaine et al., 2004).

The proposed definition of the PE presumes that the decomposition rate of the SOM pool is not constant and depends not only on environmental factors (i.e., soil temperature and moisture) but also on the dynamics of other C pools (e.g., microbial biomass, Blagodatskaya and Kuzyakov, 2008). It also presumes that the

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decomposition of C pools is interdependent and not additive. Both of these statements contrast with the traditional concept that SOM decomposition is solely temperature- and moisture-driven, a concept that is used in most models simulating C and N dynamics in soil (reviewed by Molina and Smith, 1998; Smith et al., 1998; Manzoni and Porporato, 2009). However, many experimental studies have shown that the degradation rates of organic substances depend on microbial community composition, size, and physiology – the parameters that directly affect enzyme activity in soil (Schimel and Gulledge, 1998; Balser and Firestone, 2005; Wall and Moore, 1999; Zogg et al., 1997; Griffiths et al., 2008; Paterson et al., 2009). In the last decade, modelers have therefore considered microbial biomass as a driving force of decomposition (Blagodatsky and Richter, 1998; Gignoux et al., 2001; Schimel and Weintraub, 2003; Müller and Höper, 2004; Fontaine and Barot, 2005), and they have applied decomposition equations with non-linear rate dependencies, as reviewed by Manzoni and Porporato (2009). These models presented the theoretical possibility of simulating PEs but the model outputs have never been tested using experimentally measured PE dynamics upon application of ^{14}C or ^{13}C label. The application of ^{14}C or ^{13}C label allows researchers to distinguish the CO_2 that evolves from the applied substrate and from native SOM pools.

Modeling approaches capable of predicting PE in soils have periodically appeared in the literature since the 1970s (Parnas, 1976; Smith, 1979). In recent years, this topic has been addressed more frequently because of rising interest in feedbacks in the terrestrial C cycle and in controls of soil heterotrophic respiration (Fontaine and Barot, 2005; Moorhead and Sinsabaugh, 2006; Neill and Gignoux, 2006). The models capable of describing PE differ in concept as well as in complexity (rate equations and number of model parameters; reviewed by Wutzler and Reichstein, 2008; Manzoni and Porporato, 2009). Wutzler and Reichstein (2008) showed that the long-term consequences of decomposition formulations differ qualitatively depending on representation of the active decomposers. These authors compared mathematical expressions that describe SOM decomposition rates for their suitability for PE simulation. Studies of Wutzler and Reichstein (2008) and Fontaine and Barot (2005) clearly demonstrated that PE can be properly modeled if the decomposition rate depends not only on the SOM amount, but also on a second pool, namely microbial biomass. Therefore, we developed and applied a model based on biotic drivers of SOM decomposition and substrate utilization by microbial biomass. The specific features and advantages of the new model, which is described in this paper, can be best illustrated by comparing the new model with known models. In the current study, we have compared our new approach for PE modeling with three other models of similar complexity. The models were tested using experimental data on CO_2 and microbial biomass dynamics measured both for ^{12}C and ^{14}C pools.

The present study was designed to: 1) develop a simple model allowing simulation of PEs, 2) parameterize the model based on the experimental data on the PE induced by adding ^{14}C -glucose, and 3) compare the proposed approach with three alternative models analogous to those published previously. The models were tested for their capability to describe the dynamics and size of experimentally measured PE.

2. Materials and methods

2.1. Model description

The proposed model was kept as simple as possible, and in its simplest version describes three pools of organic C (Fig. 1): soil organic C (SOC), dissolved organic C (DOC), and microbial biomass C (MB). The DOC pool is labeled using ^{14}C -glucose at the beginning of the incubation. The other two pools (MB and SOC) are unlabelled.

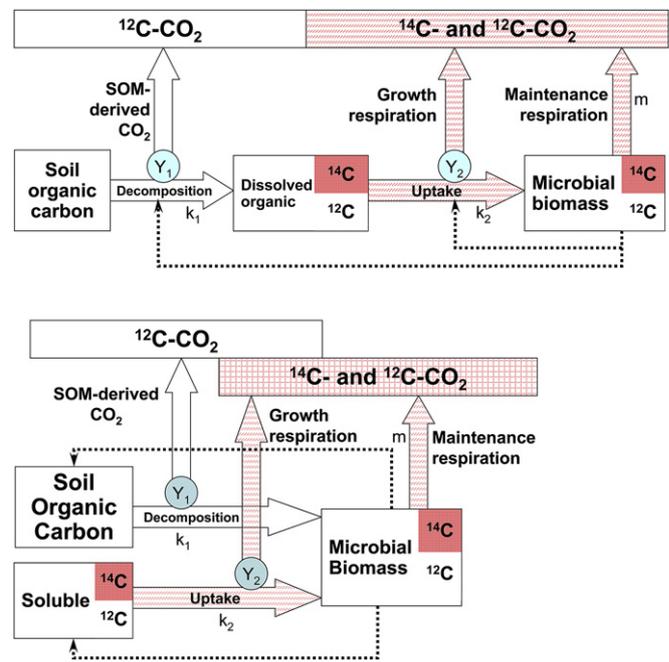


Fig. 1. Block-schemes of two alternative simulation models for describing priming effects in soil: sequential (top) or parallel (bottom) utilization of substrates with contrast availability. Carbon flows are shown as arrows, colored (hatched) blocks and arrows designate pools and fluxes labeled by ^{14}C . The dotted lines show the effect of microbial biomass amount and activity on the rates of SOM decomposition and uptake of soluble substrates. k_1 , k_2 – rate coefficients, m – maintenance coefficient; Y_1 and Y_2 – the efficiency (splitting) factors, determining which part of the C flow is respired as CO_2 . See text for detailed explanations.

The basic proposed model (referred to as model 1, Fig. 1, sequential scheme) considers decomposition as a sequential process, i.e., organic substrates must first be solubilized before they become available to microorganisms. According to this model, the decomposition rate of SOC depends on the amount of microbial biomass and the rate coefficient k_1 :

$$\frac{d\text{SOC}}{dt} = -k_1 \cdot \text{MB} \quad (1)$$

This dependency assumes that decomposition is regulated by extracellular enzymes, which, however, are not explicitly included in the model for the sake of simplicity. The C flux by SOC decomposition is divided to DOC and CO_2 according to efficiency factor Y_1 . Thus, corresponding portions of C enter the DOC and CO_2 pools. The rate of DOC change in time is:

$$\frac{d\text{DOC}}{dt} = Y_1 \cdot k_1 \cdot \text{MB} - k_2 \cdot \text{DOC} \cdot \text{ACT} \cdot \text{MB} \quad (2)$$

The first part of the right side of Eq. (2) corresponds to the fixed portion of decomposition flow (Eq. (1)). DOC can be directly taken up by microorganisms (second part of the right side of Eq. (2)). The DOC consumption rate depends on 1) microbial activity status (ACT, Eq. (5), described in detail later), 2) microbial biomass amount (MB), and 3) the substrate amount (DOC) multiplied by the rate constant k_2 . The consumed C is used for microbial growth and respiration according to the efficiency factor Y_2 as described in Eq. (3) (first part of right side).

$$\frac{d\text{MB}}{dt} = Y_2 \cdot k_2 \cdot \text{DOC} \cdot \text{ACT} \cdot \text{MB} - m \cdot \text{ACT} \cdot \text{MB} \quad (3)$$

The active part of the microbial biomass ($\text{ACT} \times \text{MB}$) decreases due to maintenance respiration (second part of the right side of

Table 1
Initial conditions for the models describing priming effects in soil.

Variable, description and equation number	Initial value, units	Method of estimation (details are in the Material and methods section)
t: time (1–5, 9, 11)	0, hours	Independent variable
SOC: Insoluble soil organic matter (1)	21.3 (mg C g soil ⁻¹)	Experiment, total soil C
DOC: Dissolved organic carbon (2) or (2a)	0.01 (mg C g soil ⁻¹) 1.01 (mg C g soil ⁻¹)	Experiment, unamended soil Experiment, soil amended with labeled glucose 1.0 mg C (g soil) ⁻¹
MB: Soil microbial biomass (3)	0.6 (mg C g soil ⁻¹)	Experiment, unamended soil
CO ₂ : Respired CO ₂ (4)	0 (mg C g soil ⁻¹)	Zero at start
ACT: Microbial activity status (5) (ACT is not included in models 1a and 2a)	0.0585 (undimensional)	Adopted from Blagodatsky and Richter (1998)

Eq. (3)). The replenishment of SOC by dead microbial residues is not considered in our model for the sake of simplicity. This omission is acceptable in the case of short-term experiments (such as in our study). The mineralization of SOM (Eq. (1)), microbial growth and maintenance (Eq. (3)) lead to CO₂ production:

$$\frac{dCO_2}{dt} = (1 - Y_1) \cdot k_1 \cdot MB + (1 - Y_2) \cdot k_2 \cdot DOC \cdot MB \cdot ACT + m \cdot ACT \cdot MB \quad (4)$$

The first part of right side of Eq. (4) is equal to the fixed portion of the SOC decomposition rate (cf. Eq. (1)). The second part of right side in Eq. (4) represents the microbial growth respiration and is equal to the fixed portion of microbial uptake of DOC (cf. Eq. (2)). Maintenance respiration is described by the third part of the right side of Eq. (4), which corresponds to the second part of the right side in Eq. (3).

The final equation (5) in our model describes the dynamics of microbial activity (ACT), which depends on the DOC concentration:

$$\frac{dACT}{dt} = k_2 \cdot DOC \cdot \left(\frac{DOC}{DOC + k_3} - ACT \right) \quad (5)$$

The activity function (for detailed description see Blagodatsky and Richter, 1998) takes values in the range $0 < ACT < 1$, if initial values of ACT are in the range [0,1]. The current value of ACT shows the proportion of the total microbial biomass that is actively growing. The activity status of microbial biomass depends on amount of available substrate (DOC), and its dynamical changes depend on Michaelis–Menten type response function ($DOC/(DOC + k_3)$), where parameter k_3 (inhibition constant for C-dependent microbial activity) determines the microbial reaction rate as a function of changes in DOC amount.

The initial values for model variables (Table 1) were obtained experimentally in the current study (Eqs. (1)–(4)) or borrowed from literature (Eq. (5)). The described model has a total of six parameters (Table 2, model 1) applied without modifications for all tested treatments, namely: 1) dynamics of C pools in control (unamended

soil, 2) dynamics of unlabelled ¹²C in soil amended with glucose as described in the experimental design section, and 3) dynamics of ¹⁴C-labeled pools in amended soil (Fig. 1). In the latter case, ¹⁴C-glucose enters the system as a part of the DOC pool at the beginning of the experiment, and then all reaction rates and ¹⁴C transfer are calculated according to the same equations as for ¹²C.

To evaluate the advantages and shortcomings of the suggested model, as well as to compare it with the previous formulations (Fontaine and Barot, 2005; Neill and Gignoux, 2006), we also tested an alternative model concept, which is referred to as model 2 (Fig. 1, bottom). In contrast to model 1, which has a sequential decomposition scheme, model 2 has a parallel decomposition scheme in which C flows directly from different organic sources to microbial biomass without solubilization. All rate expressions in model 2 are the same as in model 1. The only difference between model 2 and model 1 is the transfer of the first term on the right side of Eq. (2) (soluble substrate input) to Eq. (3), i.e., direct input of C from insoluble SOM to the microbial biomass. So, for the parallel decomposition scheme in model 2, equations for DOC and for MB are:

$$\frac{dDOC}{dt} = -k_2 \cdot DOC \cdot ACT \cdot MB \quad (2a)$$

$$\frac{dMB}{dt} = Y_1 \cdot k_1 \cdot MB + Y_2 \cdot k_2 \cdot DOC \cdot ACT \cdot MB - m \cdot ACT \cdot MB \quad (3a)$$

2.2. Calculation of the priming effect

Based on experimental data and model runs, we calculated PE using several approaches. Cumulative PE, expressed in mg C per g soil, was:

$$PE = {}^{12}CO_2^{\text{amended}} - CO_2^0, \quad (6)$$

where ¹²CO₂^{amended} is unlabelled ¹²C–CO₂ evolved from soil amended with ¹⁴C–glucose and nutrients, and CO₂⁰ is unlabelled

Table 2

Optimized parameters for the alternative models tested. Model versions 1a and 2a were run without activity function (Eq. (5)). Correspondingly, the variable ACT equals to 1 and remains constant in eqs. (1)–(4) for model versions 1a and 2a.

Parameter description	Units	Model tested			
		1	1a	2	2a
		Parameter value			
Decomposition constant for SOC, k_1	day ⁻¹	0.019	0.019	0.020	0.023
Second-order rate constant for microbial C uptake, k_2	g mg C ⁻¹ day ⁻¹	6.59	1.14	6.91	0.82
Inhibition constant for C-dependent microbial activity, k_3	mg C g ⁻¹	2.64	not included	4.72	not included
Maintenance coefficient, m	day ⁻¹	0.5	0.0082	0.2	0.0005
Efficiency of decomposition, Y_1	mg C mg C ⁻¹	0.02	0.02 ^a	0.02	0.02 ^a
Efficiency of substrate uptake, Y_2	mg C mg C ⁻¹	0.62	0.52	0.46	0.44

^a Parameter Y_1 violated its constraint range (0.0) during the optimization procedure.

^{12}C - CO_2 evolved from soil without substrate addition. The relative intensity of PE was estimated as a percentage of changes relative to the unlabelled CO_2 production with and without substrate addition by:

$$\text{PE\%} = \frac{{}^{12}\text{CO}_2^{\text{amended}} - \text{CO}_2^0}{\text{CO}_2^0} \cdot 100\% \quad (7)$$

PE calculated using Eqs. (6) and (7) can be derived from both experimental data and from model output. In addition, the proposed model allows us to split CO_2 -based PE into apparent PE and real PE (Blagodatskaya et al., 2007). Thus, the relative difference between the first parts of the right side of Eq. (4) for amended and unamended soil is a **real PE** caused by changes in SOM decomposition:

$$\text{real PE\%} = \frac{\text{SOC derived } {}^{12}\text{CO}_2^{\text{amended}} - \text{SOC derived } \text{CO}_2^0}{\text{SOC derived } \text{CO}_2^0} \cdot 100\% \quad (8)$$

where SOC-derived CO_2 was calculated by integrating the first part of equation (4) for the corresponding unlabelled pool of microbial biomass:

$$\frac{d(\text{SOC derived } \text{CO}_2)}{dt} = Y_1 \cdot k_1 \cdot \text{MB} \quad (9)$$

The relative difference between the third part of the right side of Eq. (4) for amended and unamended soil (unlabelled C) is due to intensification of microbial metabolism (maintenance respiration) in amended soil or **apparent PE**:

$$\text{apparent PE\%} = \frac{\text{maintenan } {}^{12}\text{CO}_2^{\text{amended}} - \text{maintenan } \text{CO}_2^0}{\text{maintenan } \text{CO}_2^0} \cdot 100\% \quad (10)$$

where CO_2 evolved due to maintenance respiration was calculated by integrating the third part of Eq. (4) for the corresponding unlabelled pool of microbial biomass:

$$\frac{d(\text{maintenan } \text{CO}_2)}{dt} = m \cdot \text{ACT} \cdot \text{MB} \quad (11)$$

2.3. Model evaluation and statistics

The model described in Table 1 by Eqs. (1)–(5) was built using MODELMAKER[®] Version 3.0.3 software (ModelMaker, 1997). Parameters were optimized and goodness-of-fit statistics were generated by procedures included in this software package. To evaluate the capacity of the proposed models to simulate labeled and unlabelled CO_2 efflux from both control soil and soil amended with glucose and nutrients, we compared the following statistical criteria: (1) r^2 , the fraction of total variation explained by the model defined as a ratio of model weighted sum of squares (WSS) to total weighted sum of squares; and (2) variance ratio or *F*-value calculated as follows:

$$F = \frac{\left(\frac{\text{model WSS}}{\text{DF}}\right)}{\left(\frac{\text{residual WSS}}{\text{DF}}\right)} \quad (12)$$

where residual WSS was calculated as a difference between total WSS and model WSS, and DF is degrees of freedom ($\text{DF} = n - 1$) with n equal to the number of parameters in the model or the

number of data points for numerator and denominator in Eq. (12), respectively.

2.4. Experimental design and analytical methods

For the model calibration, we used experimental data obtained in an incubation study of the Ah of a loamy Haplic Luvisol ($C_{\text{org}} = 2.4\%$; $N_{\text{total}} = 0.2\%$, $\text{pH}(\text{CaCl}_2) = 5.1$). Thirty-gram (dry weight) sub-samples of moist soil were weighed and put into 250-ml Schott jars. After the soil was pre-incubated at 22 °C for 24 h, a solution containing glucose (1 mg C g⁻¹ soil) and mineral nitrogen as $(\text{NH}_4)_2\text{SO}_4$ (C:N = 10:1) was added to the soil so that the final moisture content was 60% of water holding capacity. After glucose and N were added to the soil, one small vial containing 3 ml of 1 M NaOH was placed in each incubation jar to trap CO_2 . The jars were then closed air-tight and incubated for 54 days at 22 °C and with the soil at 60% of WHC. At 2, 7, 12, and 24 h after glucose addition and daily thereafter (with some exclusions), the vials were removed and replaced by fresh vials containing 3 ml of 1 M NaOH. After 1, 3, 7, 14, 33, and 54 days of treatment with glucose, three replicate incubation jars were used to estimate the microbial biomass by the fumigation–extraction method.

The PE was measured as the difference between unlabelled ^{12}C - CO_2 efflux from soil with and without glucose addition (Eqs. (6) and (7)). To distinguish between CO_2 originating from SOM and from added glucose, ^{14}C uniformly labeled glucose (Amersham[®]) was used. The CO_2 that evolved from the soil was trapped in the vials containing 3 ml of 1 M NaOH. The total amount of CO_2 trapped in the vials was analyzed by titration with 0.1 M HCl against phenolphthalein. Glucose-derived CO_2 was calculated according to the ^{14}C activity in NaOH, which was analyzed with a liquid scintillation counting (MicroBeta, Perkin Elmer).

Microbial biomass was estimated by the fumigation–extraction (FE) method (Vance et al., 1987) with small modifications. Briefly, fumigated (24 h, ethanol-free CH_2Cl_2) and non-fumigated soil samples (5 g) were extracted with 20 ml of 0.05 M K_2SO_4 , and the C content was determined with a DOC/DON analyzer (Multi N/C 2100, Analytik Jena, Germany). A k_{ec} -factor was calculated based on the ^{14}C budget as described by Bremer and Van Kessel (1990):

$$k_{\text{EC}} = \frac{{}^{14}\text{C}_{\text{fum}} - {}^{14}\text{C}_{\text{soluble}}}{{}^{14}\text{C}_{\text{applied}} - {}^{14}\text{C}_{\text{soluble}} - {}^{14}\text{CO}_2} \quad (13)$$

where the amount of ^{14}C additionally extracted after chloroform fumigation is represented by the nominator and the amount of ^{14}C in microbial biomass is represented by the denominator (indicates applied ^{14}C as glucose minus soluble C not consumed by microbial biomass minus respired ^{14}C - CO_2). This equation is valid only for short-term experiments (as in our study), when the incorporation of ^{14}C into humic substances can be ignored.

Labeled microbial biomass (in $\mu\text{g C g}^{-1}$) was calculated using the variable k_{ec} -factor determined for the corresponding incubation time. The total microbial biomass C in both amended and unamended soil was calculated with the constant k_{ec} -factor equal to 0.27, which was the maximal experimentally determined value for this soil when 100 $\mu\text{g C}$ -glucose g⁻¹ soil was applied.

The ^{14}C activity of microbial biomass was determined as described above after 2 ml of the K_2SO_4 extract was mixed with 4 ml of scintillation cocktail Rothiscint-Eco (Carl Roth, Germany). The glucose-derived microbial C was calculated based on ^{14}C activity in the microbial biomass divided by the ^{14}C specific activity ($^{14}\text{C}/\text{C}$) of the added glucose.

The experiment was conducted with four replications. The standard error of the means is presented in the figures.

3. Results

3.1. Measured and simulated CO₂ production

The results showed typical CO₂ efflux from soil amended with an easily available substrate (Fig. 2): the cumulative curve of CO₂ efflux is shown in the upper panel of Fig. 2, and the calculated respiration rates are shown in the lower panel of Fig. 2. The initial short-term CO₂ flush that peaked on the first day was mainly due to the fast consumption of glucose and its decomposition to ¹⁴CO₂. Only about 1% of the added ¹⁴C was found as soluble C 1 day after glucose addition. This CO₂ flush was not observed in unamended soil; in Fig. 2 (top), the thin dashed lines indicate simulation results, and the triangles indicate measured data. The remarkable difference between total and labeled CO₂ efflux was evident even during the first days after glucose amendment due to differences in total and labeled CO₂ production rates (Fig. 2, bottom). This rate difference persisted during the duration of our 54-day experiment, leading to

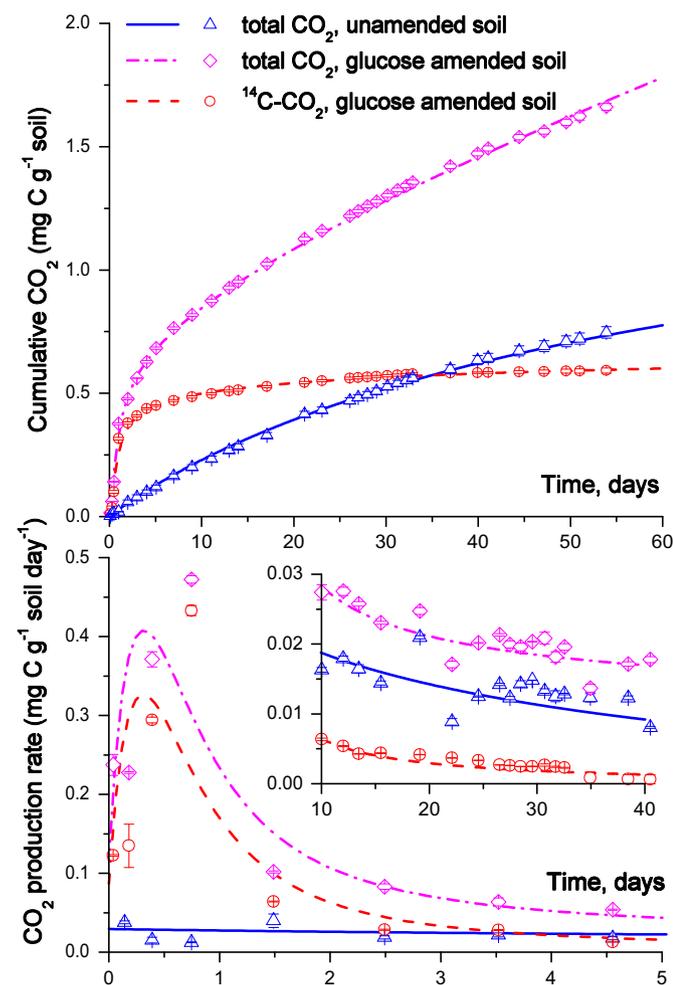


Fig. 2. Cumulative CO₂ efflux (top) and CO₂ efflux rate (bottom) from soil during 54 days of incubation. Measured data are presented as symbols: diamonds indicate total C in soil amended with glucose and nutrients, open circles indicate ¹⁴C in soil amended with glucose and nutrients, and triangles indicate total C in unamended soil; lines indicate simulation results (model 1, Eq. (4)) run for ¹⁴C and ¹²C both in glucose-amended and unamended soil. Embedded picture in bottom panel presents the longer-term rate dynamics.

the large difference in cumulative curves (Fig. 2, top). For total CO₂ efflux, slopes of cumulative curves and rates after 10 days clearly differed between unamended (control) soil and soil amended with glucose (Fig. 2). Therefore, glucose addition caused the changes in mineralization rates of unlabelled C (i.e., glucose caused a PE).

3.2. Microbial biomass dynamics

The quantity of applied glucose (1 mg C per g of soil) was approximately twice the microbial biomass in the original soil. This made it possible to detect significant biomass increase after glucose application (Fig. 3). Microbial biomass (as estimated by the FE method) peaked after glucose amendment but did not peak in the control soil (Fig. 3). The difference in microbial biomass was less distinct than the difference in the respiration rate, and decreased gradually after 10 days. This drop in microbial biomass was satisfactorily reflected by the model. The measured biomass C was not used for parameter optimization during model calibration and comparison. Therefore, the model fit for biomass C was worse than the fit for the cumulative CO₂ data (cf. Fig. 2, top and Fig. 3). The best correspondence between the simulation and measurements was for ¹⁴C biomass, where a variable k_{ec} -factor was applied. In this case, the mismatch between model and measured data was observed mainly in the first 3 days. Our simple model probably could not perfectly reflect the rapid glucose transport in microbial cells, which proceeds faster than the process of complete glucose utilization with ¹⁴C incorporation into the structural cell constituents (Nguyen and Guckert, 2001). The time lag between fast glucose uptake by microbial biomass in the first 2 days and increase in respiration rate cannot be perfectly simulated by applied models: this is the reason for mismatch between data and simulation for respiration rates during the first 36 h. The discrepancy between model prediction and total biomass dynamics starting from the second week of incubation might also be due to model simplification (i.e., the model does not consider microbial mortality) or the assumption of a constant k_{ec} -factor for the total biomass.

3.3. Apparent and real priming effect

The increase in unlabelled CO₂ production after ¹⁴C-glucose application over the short and long term (Fig. 2, bottom, the inset) was modeled by considering two flux components of CO₂ evolved

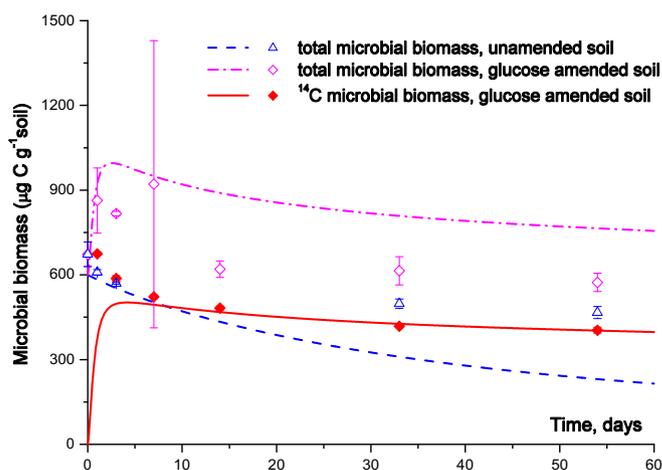


Fig. 3. Dynamics of microbial biomass measured by the fumigation–extraction method (symbols) and simulated by model 1 (lines) in soil amended with glucose and nutrients (diamonds) and in control unamended soil (triangles). Dynamics of microbial biomass labeled by ¹⁴C are indicated by filled symbols (measured) and straight line (simulated).

from soil. The unlabelled short-term flux (CO_2 peak during the first day, Fig. 2, bottom) was caused by intensified microbial metabolism (apparent PE, Eq. (10)), expressed in our model as higher maintenance respiration (last term on the right side of Eqs. (3) and (4), Fig. 4). This concept links maintenance respiration with actively metabolizing microbial biomass (Blagodatsky and Richter, 1998; van Bodegom, 2007).

The increase in unlabelled CO_2 efflux from the glucose-amended soil persists after the initial CO_2 peak (Fig. 2, top) because of the higher total microbial biomass in amended versus control soil (Fig. 3, Eq. (3)). Thus, the increase in microbial biomass C caused by adding glucose in the first days boosts the SOM decomposition rate (Eq. (1) and first term on right side of Eq. (4), Fig. 5) and consequently the efflux of unlabelled CO_2 even when the glucose was already exhausted. The higher microbial activity and the linked increase in maintenance expenses stopped 4 days after glucose amendment, so maintenance respiration in glucose-amended soil fell even lower than the corresponding values for unamended soil (Fig. 4). This means that the PE after the 4th day is real PE, i.e., the PE was caused by SOM decomposition (compare decomposition curves in Fig. 4) and not merely by the activated respiration of dormant microbial biomass. The relative contribution of different fractions of respired CO_2 as well as microbial biomass and DOC dynamics are presented as model outputs for labeled (top) and unlabelled C pools both in glucose-amended (middle) and unamended (bottom) soil in Fig. 5. The quantity of CO_2 respired during SOM decomposition is larger in glucose-amended versus unamended soil (cf. middle and bottom panels), while the quantity of CO_2 respired during maintenance is larger in unamended soil. In the latter case, the difference corresponds to the more distinct microbial biomass decrease in unamended versus glucose-amended soil (Fig. 3).

Cumulative PE calculated according Eq. (6) and based on experimental data was reasonably described by the model with optimized parameters (Fig. 6, top; Table 2). The proposed model untangles the typical two-stage dynamics of PE: apparent PE dominated in the beginning and real PE dominated after about 14 days. The different contribution of apparent and real PE to the dynamics of total PE can be better presented if the relative changes of cumulative PE (Eqs. (7),(8),(10)) are expressed as percentages and plotted against time (Fig. 6, bottom). Immediately after glucose application, both real and apparent PE quickly increased, but

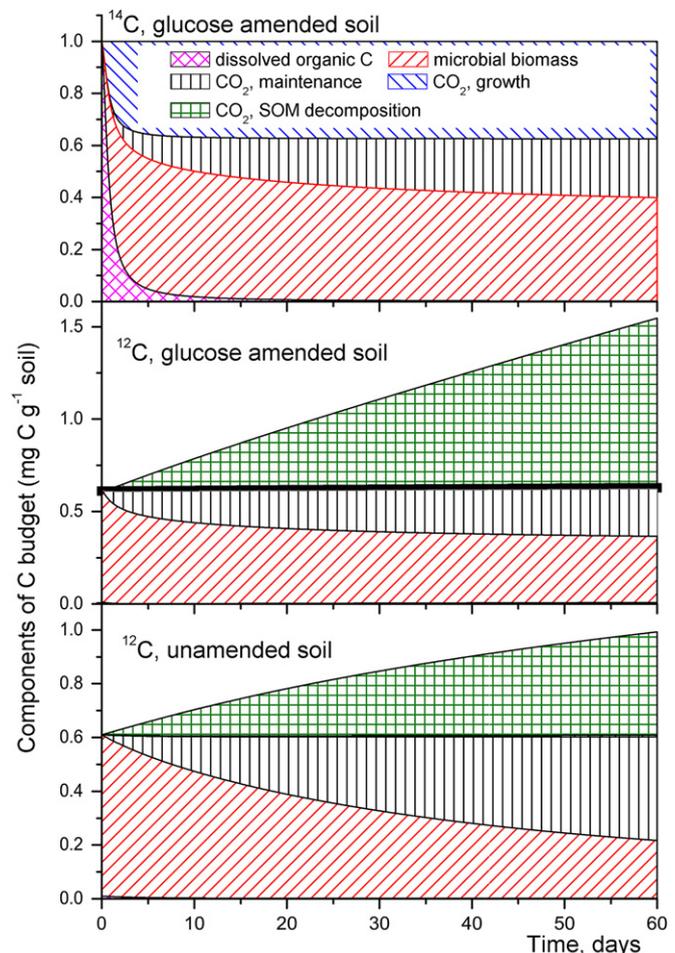


Fig. 5. Dynamics of C pools in soil simulated by model 1 (mass-balance data). ^{14}C in glucose-amended soil (top), ^{12}C in glucose-amended soil (middle), and ^{12}C in unamended soil (bottom) are shown as dissolved organic carbon (DOC), microbial biomass (MB), CO_2 respired by maintenance (CO_{2_maint}), CO_2 respired by growth (CO_{2_growth}), and CO_2 respired during SOM decomposition (CO_{2_decomp}). DOC and CO_{2_decomp} are not seen in middle and bottom panels because of low values.

apparent PE was much higher (220% of CO_2 efflux in the control), while real PE reached 50%. After the maximum was reached on the first day, apparent PE sharply decreased, approaching negative values in 18 days. At the same time, real PE continued to increase, but more gradually than in the first 3 days. As a result, real PE dominated the total PE dynamics over the long term (weeks and first months). Total relative PE reached a maximum (153% of control) on the third day because of the peaking of apparent PE. On the 6th day after glucose amendment, real PE reached the values of apparent PE: all three curves on the lower part of Fig. 6 are crossed. Thereafter, SOM decomposition was the main source of extra CO_2 production because of real PE, which reached its relative maximum values (139% of control) at the end of the experiment.

4. Discussion

4.1. Essentials of the proposed PE model: active microbial biomass and microbial uptake of soluble substrates

CO_2 production in soil, i.e., the final stage of decomposition, is largely the result of microbial activity. Chemico-physical processes such as absorption–desorption and diffusion only modify the temporal and spatial patterns of the final CO_2 emission originally

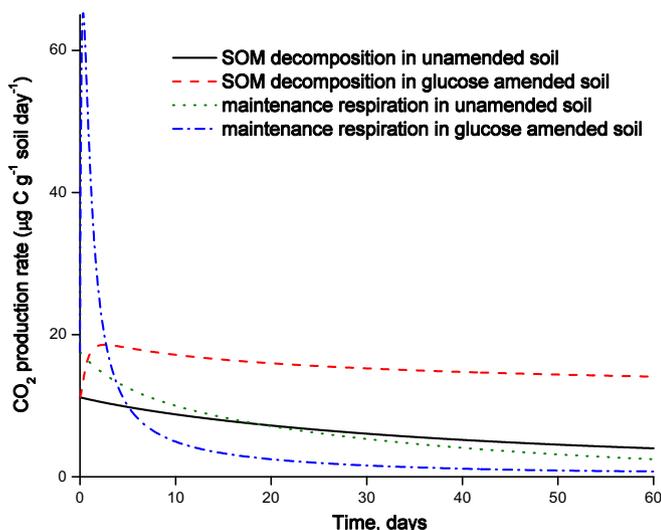


Fig. 4. Rates of CO_2 efflux from unamended soil and from soil amended with glucose and nutrients divided according to model 1 (Eq. (4)) into decomposition flux from insoluble organic matter and maintenance respiration of soil microorganisms.

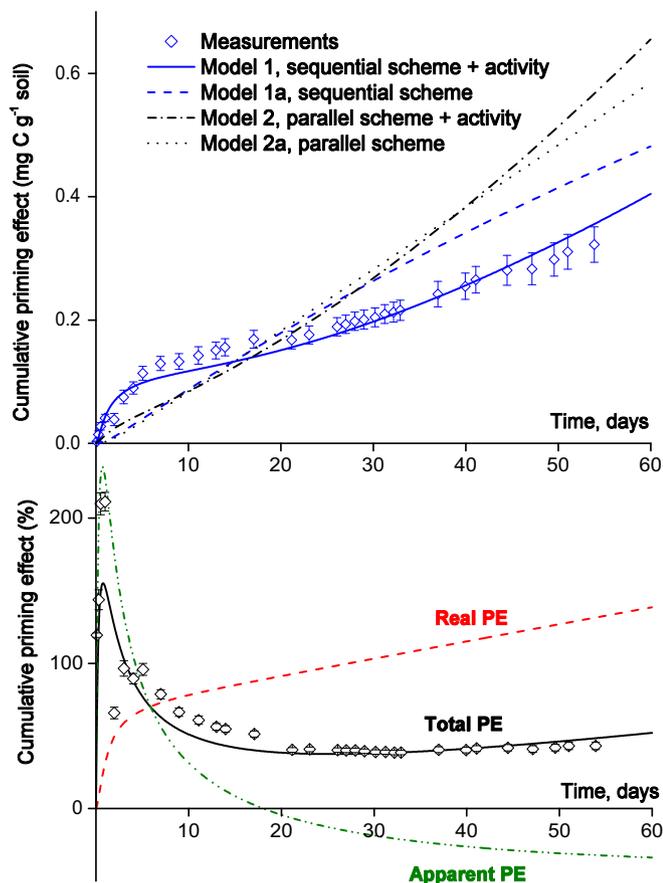


Fig. 6. Priming effect as measured experimentally and as simulated by different model approaches: cumulative priming effect (Eq. (6), top) and relative cumulative priming effect (bottom) expressed as a percentage of CO_2 efflux in the unamended soil (Eq. (7)) and its fractions: 1) apparent priming effect calculated from maintenance respiration (Eq. (8)), and 2) real priming effect caused by difference in decomposition of insoluble SOM (Eq. (10)).

produced by microorganisms (Kuzyakov et al., 2009). That is why a biologically sound model should explicitly include microbial biomass (or the active part of the biomass) in the rate regulation. We include in the proposed model the biomass pool that has stable long term behavior and does not disappear in the absence of available C. This stability is provided by including the activity function ACT (r in Blagodatsky and Richter, 1998), which slows microbial metabolic processes (i.e., maintenance) by substrate exhaustion.

SOM decomposition (CO_2 evolution) can be described mathematically by the sum of first-order decay functions. The decomposition rate of each separate SOM pool is a product of its size and the constant rate coefficient in such models (Parton et al., 1987; Whitmore, 1996b; Niklaus and Falloon, 2006; Manzoni and Porporato, 2007). This approach, which has been applied in most SOM models (reviewed by Manzoni and Porporato, 2009), assumes that microbial biomass is constant, and microbial biomass is implicitly included in the rate coefficient. In this case the decomposition rate is determined by the quantity of organic substrate plus a combination of at least three independent factors, each of which can be modeled explicitly: 1) chemical structure and decomposability of substrate (plant residues or SOM) (Moorhead and Sinsabaugh, 2006), 2) amount of active microbial biomass associated with and degrading the defined pool (Grant et al., 1993; Whitmore, 1996a), and 3) the physical probability that the microorganisms will interact with the defined SOM pool (Six et al., 2002; Masse et al., 2007). In reality, all these factors are not constant in

time, and this makes it difficult to find a unique parameter value applicable for various soils and to link a fitted parameter with measured chemical and physical soil properties or with biological features of microorganisms associated with decomposing substrate.

If the biological nature of decomposition is modeled explicitly, the model must include basic knowledge about microorganism–substrate interactions. First, modelers should recognize that microorganisms can take up and consume only dissolved substances. Therefore, the main importance of DOC (or DOM in some papers) is not because it can leach from the soil (as stated in many studies) but because it is the only stage of organic matter available for microorganisms. This leads to the emergence of an additional new (but real!) pool of dissolved organic matter. This model complication is more than compensated for by the possibility to use all knowledge about quantitative microbiology in the SOM models. Omitting this feature for the sake of simplicity corrupts the mechanistic (biological) background of the model. It also decreases the flow/variable numbers that could be experimentally verified.

4.2. Comparison of concepts in PE modeling: sequential versus parallel decomposition schemes

When modeling a complex system (such as a chain of biological transformations in soil), several alternative concepts can be used (Jans-Hammermeister and McGill, 1997). The final choice of the most appropriate model can be made after assessing the adequacy of model approaches against experimental data. Accordingly, our proposed model (Fig. 1, top) was compared with three alternative models by fitting model output to the same data set generated by our incubation experiment. These simple alternative formulations were extracted from published models based merely on evidence from experimental observations. The selection was limited to approaches that we considered to be as simple as possible, i.e., approaches that could be used in larger ecosystem models with lower spatial and temporal resolution. Concepts with complicated, fine interrelationships cannot be validated when used in models at the regional and global scale.

Several models, e.g., that of Fontaine and Barot (2005), apply parallel decomposition schemes. In this case, flows from substrates of different decomposability go directly to microbial biomass, allowing a constant portion of these fluxes to be evolved as CO_2 . In the current paper, parallel decomposition is represented in models 2 and 2a (Fig. 1, bottom, Tables 2 and 3). The model of Schimel and Weintraub (2003) applies sequential decomposition scheme, as do models 1 and 1a in the current study (Tables 2 and 3). In this case, microorganisms can take up only soluble C, which is released during decomposition of insoluble SOM. The statistical comparison of simulated and measured data for the our proposed model and the three alternative models is shown in Table 3. The sequential scheme (Fig. 1, top) performs better than the parallel scheme (Fig. 1, bottom) in describing our experimental data (cf. 1 and 2 or 1a and 2a). Both r -squared and the F-factor, which account for the model complexity, were the best for model version 1 (Table 3). When optimizing parameters in models 2 and 2a, ModelMaker tends to minimize parameter Y_1 , setting it to zero, i.e., it tends to mineralize SOM without the inclusion of C in microbial biomass. This means that according to the measured dynamics of labeled and total CO_2 , SOM cannot serve as a direct growth substrate for microorganisms. This simulation exercise confirms a basic fact from microbiology: microorganisms consume substrates insoluble form. It shows the conceptual advantage of the sequential decomposition scheme.

The model of Neill and Gignoux (2006) also describes decomposition as a two-step sequential process. This is an essential feature common with our approach (and with the model of Schimel and Weintraub, 2003). There are substantial differences, however,

Table 3
Summarized evaluation of the approaches tested for priming effect modeling.

Decomposition concept	Model	Activity state of microbial biomass (ACT)	Priming effect features	Goodness of fit for 3 measured CO ₂ pools ^a	
				r ²	F
SOM is decomposed to soluble OM, which is consumed by microbial biomass (sequential scheme, Fig. 1, top)	1	Included	Initial rate peak and second increase over the long term	0.999	22 022
	1a	Not included	No rate peaks, the rate increase with saturation	0.982	1714
SOM is directly taken up by microbial biomass (parallel scheme, Fig. 1, bottom)	2	Included	Initial flat rate peak and second increase over the long term	0.974	839
	2a	Not included	No rate peaks, the rate increase with saturation	0.959	723

^a ¹⁴C–CO₂ and total CO₂ from glucose-amended soil and total CO₂ from unamended soil.

in the biochemical background of the rate equations used in these models. The Neill and Gignoux (2006) model is based on concurrent enzyme–substrate interactions, in which soil microbial biomass is treated as the enzyme unit building the complex with SOM. The first step (biomass complexing with substrate) is a reversible and faster (not rate limiting) process, while the second step (product and “biomass–enzyme” release) is irreversible and rate-limiting for the whole decomposition process. The mathematical formulation borrowed by these authors from microbial biochemistry is applicable for describing intercellular substrate conversion by microorganisms. From our point of view, however, it is inappropriate for describing extracellular enzymatic decomposition of insoluble SOM, leading to the production of soluble organics directly available to microorganisms. Contrary to the concept of Neill and Gignoux (2006), the initial step of SOM decomposition in soil is rate limiting and irreversible (see for example Schimel and Weintraub (2003) or Moorhead and Sinsabaugh (2006)). Our model approach is a simplification of real soil biochemical dynamics, but it still can be verified against experimental data if the dynamics of DOC are measured together with extracellular enzymatic activity. We believe that our model formulation (model version 1) combines the best features of the previously published models and shows the best fit among the tested simple approaches.

4.3. Excluded features and future development: accounting for microbial mortality and an explicit exoenzyme pool

Developing a model is always directed at generalizing and synthesizing known facts. The lateral features and dependencies should be discarded, but the typical patterns of observed dynamics must be reflected by model predictions. PE is a short-term phenomenon. Accordingly, the suggested model neglects the process of microbial mortality leading to insoluble SOM accumulation. The relatively large size of SOM and the independence of the SOM decomposition rate from the size of this pool as represented in our formulation (as well as in some other models: Fontaine and Barot, 2005; Lawrence et al., 2009) makes such simplification reasonable. We observed no sharp decrease in microbial biomass after substrate exhaustion (Fig. 3). Thus, consideration of biomass losses due to maintenance respiration was sufficient to simulate this decrease. The model flexibility necessary to describe PE was obtained by including the physiological state variable. This entails an inclusion of an additional parameter (k_3) and a rate equation (Eq. (5)), but the additional parameter would also have to be added to describe mortality. Statistical estimation of best fit (Table 3) shows that the model versions incorporating the microbial activity factor describe experimental data better than the models that do not, even if the degrees of freedom (including numbers of optimized parameters) are taken into consideration (cf. *F*-values for models 1 and 1a or for models 2 and 2a in Table 3).

Another possible development of the model – one we did not include in our current formulations (model 1, Eqs. (1)–(5)) – is an

explicit description of extracellular enzyme dynamics in soil: production, accumulation, and decay of enzymes as well as their action on insoluble SOM decomposition, namely conversion of SOM into soluble forms that are directly available to the microorganisms. Several models apply a mechanistic description of enzyme turnover to simulate SOM decomposition (Schimel and Weintraub, 2003; Moorhead and Sinsabaugh, 2006; Lawrence et al., 2009). However, such models have more variables (various SOM, biomass, or enzyme pools) than those we tested here. It is difficult to measure experimentally the pool of immobilized enzymes in soil, or enzyme turnover, i.e., it is difficult to measure enzyme adsorption and decay. Because information necessary to build a realistic conceptual scheme was lacking, we rejected the explicit inclusion of extracellular enzymes in the simple PE model. Including the microbial biomass (MB) in Eq. (1) and corresponding terms of Eqs. (2) and (4) clearly presumes a microbial biomass effect on SOM decomposition through microbial production of extracellular enzymes and subsequent enzymatic action (hydrolysis, oxidation) on high-molecular compounds of SOM. Further testing of the proposed model on experimental data for soils with various physico-chemical properties (i.e., clay content), and the inclusion of temperature and moisture dependency, will be necessary if our approach is to be applied to field conditions and for longer time spans. In this case, appropriate dependencies can be added for the first rate-limiting decomposition step, thus complicating Eq. (1).

A logical development of the model would be to incorporate N limitation on the size and dynamics of PE. This is a topic of our further investigations, which are combining model developments and the experimental validation of possible relationships.

5. Conclusions and outlook

Consideration of the interactions between microbial biomass and the decomposing SOM pool in a simple model of C dynamics allows the simulation of the PE. These interactions include the regulation of SOM decomposition by the amount of microbial biomass and the regulation of microbial growth by the quantity of released soluble C. The activity of microbial biomass was included in the model as a state variable, which depends on the microbial uptake of easily available organic substances (tested here by ¹⁴C–U–glucose). The activity of microbial biomass affects both growth and maintenance respiration. This model feature allows separation of the apparent and the real PE and facilitates the description of interactions between microbial biomass and SOM at different periods after substrate addition. This is the first model that allows the simulation of the PE and its partitioning as apparent and real priming. The model was validated based on experimental data.

Incorporating PEs into the current models of C and N dynamics will increase the accordance between modeled and measured data of C and N mineralization, especially for short time scales. It will also facilitate the evaluation of the main model parameters behind SOM decomposition and microbial biomass turnover.

In contrast to most other models, our suggested model approach does not consider microbial biomass as merely a passive pool whose decomposition depends solely on environmental conditions. Microbial biomass is a direct driver of the decomposition and turnover of all other SOC pools, and its activity is a crucial parameter affecting decomposition rates. Because the activity of microbial biomass strongly depends on the presence and accessibility of available substrates, these substrates indirectly affect SOM decomposition. This calls for the inclusion of microbial biomass in the models of C and N dynamics in soil not only as a self-decomposing pool but especially as a process driver.

Acknowledgements

This research was supported by the European Commission (Marie Curie IIF project MICROSOM) and by the Alexander von Humboldt Foundation (fellowship for SB).

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