Society for
Mathematical
Biology

ORIGINAL ARTICLE

A Data-Validated Stoichiometric Model for the Priming Effect

Pablo Venegas Garcia[1] ⬤ · Hao Wang[1]

Abstract

Due to global warming, interest in sequestering carbon by appropriately managing soils has contributed to studying the dynamic exchange of carbon and nitrogen in soils and atmospheric CO_2. The priming effect, or the intensified CO_2 emissions from soil organic matter (SOM) decomposition in short periods by using labile substrates, has been a topic of interest over the last decades. A combination of two experimentally supported mechanisms explains the priming effect phenomenon, and for the first time, we combine them in a novel stoichiometric model. The model considers the effects of labile substrate utilization in soils during the SOM decomposition and how CO_2 emissions rates are affected. Laboratory data and a local sensitivity analysis validate the accuracy and robustness of the model. We find an optimized ratio of labile carbon and nitrogen that intensifies SOM decomposition for different soil features. The priming effect is weakened as C/N in SOM increases for nutrient-poor soils and is independent of C/N in SOM for nutrient-rich soils. The time required for microorganisms to decompose SOM at its maximum rate is delayed only for labile carbon treatments and poor-nutrient soils but remains constant otherwise. Finally, the SOM degradation efficiency determines the priming effect's acceleration or reduction under different soil treatments.

Keywords Priming effect · Stoichiometry · Mathematical modeling · Soil organic matter · C and N modeling

✉ Pablo Venegas Garcia
  venegasg@ualberta.ca

  Hao Wang
  hao8@ualberta.ca

1   Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton, AB T6G2G1, Canada

🖄 Springer

The potential effects of increased atmospheric carbon dioxide (CO_2) on global warming have been a matter of public interest since the industrial revolution (Lal and Follett 2009; Sylvia et al. 2005; Falkowski et al. 2000). Carbon sequestration in plant biomass and soil organic matter through appropriate management of cultivated soils is a process that can mitigate the atmospheric CO_2. By understanding the dynamical exchange of carbon and nitrogen from the atmosphere into the terrestrial ecosystems, carbon sequestration may be improved (Kuzyakov et al. 2000; Bhatti and Tarnocai 2009; Beeckman et al. 2018; Tate 1995). In particular, part of the soil scientists' efforts has been toward studying CO_2 emissions from soils due to their potential contribution to global warming. Different theories are being continuously developed to describe the linked interactions between organic matter and labile compounds as soil microbial activities (Kuzyakov et al. 2000; Blagodatskaya and Kuzyakov 2008; Kuzyakov 2010; Chen et al. 2014).

Soil organic matter (SOM) is a significant carbon reservoir and principal nutrient source for plant growth as it contributes to soil quality (Fontaine et al. 2003). SOM is a complex biological residue formed over time due to the accumulation of undecayed, recalcitrant organic matter (Lal and Follett 2009; Sylvia et al. 2005; Chen et al. 2014). SOM carbon pool is about two or three times that in the atmosphere. Thus, any changes will significantly affect the atmospheric carbon concentration levels (Sylvia et al. 2005; Manlay et al. 2007). The input of fertilizers, organic substances and plant residues may increase the microbial activity in soils, enhancing the decomposition rate of SOM in short periods. Consequently, a sudden and increased release of CO_2 from soil respiration would directly contribute to global warming (Lal and Follett 2009; Chen et al. 2014; Blagodatskaya and Kuzyakov 2008).

The priming effect is defined as the sudden increased rate of SOM decomposition, caused by the input of substrates in soils (Kuzyakov et al. 2000). This natural phenomenon and its mechanisms have been an important topic in several European countries over the last decades (Kuzyakov 2010). Despite many theories and mechanisms proposed to describe the priming effect, in this work, we consider the 'stoichiometric decomposition' and 'microbial nitrogen mining' approach (Chen et al. 2014). These mechanisms relate the SOM decomposition rate depending on the availability of labile carbon (C) and nitrogen (N) for different microbial communities. The 'stoichiometric decomposition' mechanism assumes that microbial SOM decomposition rate is at its highest when their demand of C and N is satisfied and decreases when the availability of N is limited (Hessen et al. 2004). On the other hand, the 'microbial nitrogen mining' mechanism assumes increased harvesting for N from SOM using labile C as an additional energy source to satisfy microbial growth requirements (Moorhead and Sinsabaugh 2006; Craine et al. 2007).

Different microbial communities decompose SOM at different rates depending on the availability of substrates. The linkage between the mechanisms mentioned above is due to the dynamic interaction between these microbial communities, labile carbon and nitrogen sources, and SOM (Chen et al. 2014). Soil microbial communities may be separated into two main groups despite the vast number of microbes capable of degrading SOM. Rapidly growing soil bacteria mainly involved in decomposing labile substrates are termed *zymogenous* bacteria. Now, slow-growing organisms predominantly associated with the decomposition of SOM are classed as *autochthonous* (Tate

1995). In this sense, the stoichiometric decomposition and microbial nitrogen mining mechanisms can be related to *zymogenous* and *autochthonous* bacteria, respectively (Chen et al. 2014; Hessen et al. 2004; Craine et al. 2007).

It is necessary to incorporate C and N dynamics into mathematical models to study the priming effect as the interaction between microbial communities, labile compounds, and SOM (Blagodatsky et al. 2010). To achieve this, we develop a stoichiometrical mathematical model that simultaneously considers stoichiometric decomposition and microbial nitrogen mining mechanisms. The stoichiometrical framework for our system of ordinary differential equations allows us to incorporate C and N dynamics from labile substrates as the carbon and nutrient dynamics contained in the SOM. We validate our model using a laboratory data set adapted from (Chen et al. 2014). Part of the complete laboratory data set shows how different soil treatments based on labile C and N may induce different CO_2 emission rates from soils depending on the strength of the priming effect. Including different pools to track carbon and nutrient contents in SOM as labile substrates rely on the assumption that the priming effect is governed by the availability of resources, microbial biomass and stoichiometric constraints (Drake et al., 2013; Sterner and Elser, 2017; Chen et al., 2014).

Our approach considers the balance of soil substrates as their interaction with microbial communities during the SOM decomposition process, i.e., using stoichiometry theory (Sterner and Elser 2017). We determine the robustness of the model and the crucial parameters for the priming effect with a sensitivity analysis. In this way, we investigate how soil features, such as nutrient content in SOM, delimit an optimized C/N of labile substrates to decompose SOM in terms of efficiency, the priming effect strength and the time of maximum SOM decomposition rate. Furthermore, we explore the impact of the SOM degradation efficiency on the system and how the acceleration or decrease of the priming effect is related. The model could provide insights into how using substances rich in C and N, such as green manure, for example, in different levels of nutrient richness in soils, may indirectly impact global warming by modifying the SOM degradation rates in short periods.

1 Model Formulation

To study the decomposition of SOM under aerobic conditions, we propose the following stoichiometrical mathematical model. The 'stoichiometric decomposition' and 'microbial N mining' mechanisms are continuously subject to a system of nonlinear differential equations and governed by the availability of labile compounds such as C and N. Such mechanisms are triggered implicitly by the microbial biomass growth rate and constrained by the availability of substrates. It is assumed that SOM decomposition rate increases with only adding labile C as the 'microbial N mining' mechanism suggests. Moreover, it is at its highest when the microbial biomass demand of labile C and N is satisfied as 'stoichiometric decomposition' mechanisms convey (Chen et al., 2014; Fontaine et al., 2003). In natural soil ecosystems, N is the limiting nutrient for microbial communities. To keep the model as simple as possible, we consider only C, N found in organic substances as a necessary simplification (Lal and Follett 2009;

Chen et al. 2014). Finally, the CO_2 emissions from the decomposition of organic matter are described in terms of the microbial respiration rate (Kuzyakov et al. 2000).

The microbial biomass rate of change depends on the availability of easily degradable substrates as the ability to harvest the required nutrients from SOM (Chen et al. 2014). Both microbial communities such as *zymogenous* and *autochthonous* decompose SOM at different efficiency levels, and their growth rates differ regarding the availability of labile resources (Chen et al. 2014; Blagodatskaya et al. 2007). To mathematically consider this limitation, we consider Liebig's law of the minimum, which states that the microbial growth rate is limited by the most limiting resource (Sterner and Elser 2017). To track the microbial biomass rate of change in terms of carbon units, we make use of the following equation:

$$B' = \underbrace{(\mu_c \min\{f(N), g(C)\} + \mu_s H(C) \min\{f_s(N_s), g_s(C_s)\}) B}_{\text{intrinsic growth}} - \underbrace{\epsilon B}_{\text{death}} - \underbrace{l B}_{\text{respiration}},$$

(1)

where $H(C)$ is a dimensionless saturating function that modulates the impact of a mechanism during the decomposition of SOM regarding the availability of labile C in soils. The first two terms on the right-hand side of the above equation correspond to the intrinsic microbial growth. In particular, the first term corresponds to the fast-growing *zymogenous* bacteria, and the second term to the slow-growing *autochthonous* bacteria. The minimum function is related to Liebig's law which limits the maximal microbial growth rate in terms of the available resources in the system. The dimensionless functions $f(N)$ and $g(C)$ (or simply f, and g) correspond to saturating functions which represents the N and C uptake rate, respectively (Wang et al. 2009). For simplicity, the SOM pool is divided into the amount of recalcitrant carbon C_s and nitrogen N_s, respectively. The dimensionless functions $f_s(N_s)$ and $g_s(C_s)$ (or simply f_s and g_s) are saturating functions which represents the SOM compounds degradation rates. The last two terms correspond to biomass loss by microbial death (ϵ) and respiration (l) rates.

The dynamics for the labile carbon pool are given by

$$C' = -\underbrace{\frac{\mu_c}{r_1} \min\{f(N), g(C)\} B}_{\text{labile carbon decomposition}} + \underbrace{\epsilon B}_{\text{carbon recycling}}.$$

(2)

In the above equation, the yield constant (r_1) is the proportional conversion of C to microbial biomass (Kong et al. 2018). It is also considered the immediate carbon recycling in this model by the natural death of microorganisms at a rate (ϵ).

A simplified version of a more complex process for the nitrogen dynamics is represented as follows:

$$N' = -\underbrace{\theta \mu_c \min\{f(N), g(C)\} B}_{\text{labile nutrient uptake}} + \underbrace{\theta(\epsilon + l) B}_{\text{nutrient recycling}} +$$

$$\underbrace{(\theta_s - \theta) \mu_s H(C) \min\{f_s(N_s), g_s(C_s)\} B}_{\text{nutrient exudation from SOM decomposition}}, \text{ where } \theta_s > \theta.$$

(3)

The first term corresponds to the microbial labile nutrient uptake rate to satisfy stoichiometric growth requirements. The second term represents nutrient recycling due to mass-specific microbial respiration loss and death rate (Kong et al., 2018; Alijani et al., 2015). The constant parameter (θ) corresponds to the microbial N/C ratio, and it is assumed constant since we are assuming a strict homeostasis (Sterner and Elser, 2017; Wang et al., 2012, 2018). The last term represents the nutrient exudation from SOM decomposition where (θ_s) is the N/C ratio for SOM, which is assumed constant for simplicity (Stotzky 2000; Fontaine et al. 2011).

The dynamics for recalcitrant carbon in SOM are represented as

$$C'_s = \underbrace{-\frac{\mu_s}{r_2} H(C) \min\{f_s(N_s), g_s(C_s)\}B,}_{\text{recalcitrant carbon decomposition}} \qquad (4)$$

where the yield constant r_2 is the proportional conversion of C_s to microbial biomass.

Finally, the dynamics of the recalcitrant nutrients found in SOM are described as

$$N'_s = \underbrace{-\theta_s \mu_s H(C) \min\{f_s(N_s), g_s(C_s)\}B}_{\text{nutrient uptake from SOM decomposition}}. \qquad (5)$$

In this way, microbial harvest for SOM nutrients will increase the labile nutrients availability in soils. This assumption is supported by the findings on plants allocating rich labile C substrates to microbial communities through their roots in exchange for nutrients found in SOM (Sylvia et al. 2005). Therefore, we propose the whole model as

$$
\begin{aligned}
B' &= (\mu_c \min\{f(N), g(C)\} + \mu_s H(C) \min\{f_s(N_s), g_s(C_s)\}) B - \epsilon B - lB, \\
C' &= -\frac{\mu_c}{r_1} \min\{f(N), g(C)\}B + \epsilon B, \\
N' &= -\theta \mu_c \min\{f(N), g(C)\}B + \theta(\epsilon + l)B \\
&\quad + (\theta_s - \theta) \mu_s H(C) \min\{f_s(N_s), g_s(C_s)\}B, \\
C'_s &= -\frac{\mu_s}{r_2} H(C) \min\{f_s(N_s), g_s(C_s)\}B, \\
N'_s &= -\theta_s \mu_s H(C) \min\{f_s(N_s), g_s(C_s)\}B,
\end{aligned}
\qquad (6)
$$

where the saturating functions take the Monod form, i.e.,

$$f(N) = \frac{N}{N + K_f}, \quad g(C) = \frac{C}{C + K_g}, \quad f_s(N_s) = \frac{N_s}{N_s + K_{f_s}} \quad g_s(C_s) = \frac{C_s}{C_s + K_{g_s}}, \qquad (7)$$

and $H(C)$ we will propose it as

$$H(C) = 1 - \frac{C}{C + K_h}. \qquad (8)$$

The function $H(C)$ modulates the 'microbial N mining' and 'stoichiometric decomposition' mechanism depending on the availability of labile substrates. The microbial growth will increase at high rates when the microbial stoichiometric constraints are met, potentially increasing SOM decomposition. On the other hand, with sustained utilization of labile C, the nutrient exudation from SOM decomposition is continuously increasing and is proportional to the microbial biomass. Now, emissions of CO_2 in this model are directly related to the microbial respiration rate. To model the CO_2 rate of change, we will use the following equation:

$$CO_2' = lB'. \tag{9}$$

Since we consider the model for short periods and the laboratory data used was based on a closed nutrient system, i.e., there is no loss or gain of N, we assume the conservation of mass law for N. Then, the total nitrogen (T_N) dynamics present in model (6) is given by

$$T_N' = \theta B' + N' + N_s' = 0, \tag{10}$$

for some $\theta_s > \theta$. Therefore, the total nitrogen in the system is fixed and

$$N = T_N - \theta B - N_s, \tag{11}$$

where

$$T_N = \theta B(0) + N(0) + N_s(0), \tag{12}$$

which evidently results in a simplification of system (6) if required.

2 Material and Methods

The increased atmospheric CO_2 derived from the heavy use of crop fields has led soil scientists to study the priming effect over the last decades. Several mechanisms and theories have been developed to explain this natural phenomenon. However, the combination of stoichiometric decomposition as the microbial nitrogen mining mechanisms has been supported by laboratory experiments (Kuzyakov et al. 2000; Chen et al. 2014). The laboratory experiment used to validate this model is summarized as follows.

2.1 Laboratory Experiment

The combination of the stoichiometric decomposition and microbial nitrogen mining mechanisms was experimentally supported to understand better the priming effect (Chen et al. 2014). This experiment measured different microbial growth rates, extracellular enzyme production and CO_2 emissions derived from the decomposition of labile substrates as from SOM. The experiment was based on adding different soil

Table 1 Experimental design. Table adapted from (Chen et al. 2014)

Treatment	Amount (μg C g soil^{-1})	Applied N (μg N g soil^{-1})
Control	0	0
min-N	0	110
Suc-C	500	0
Suc-C+min-N	500	110
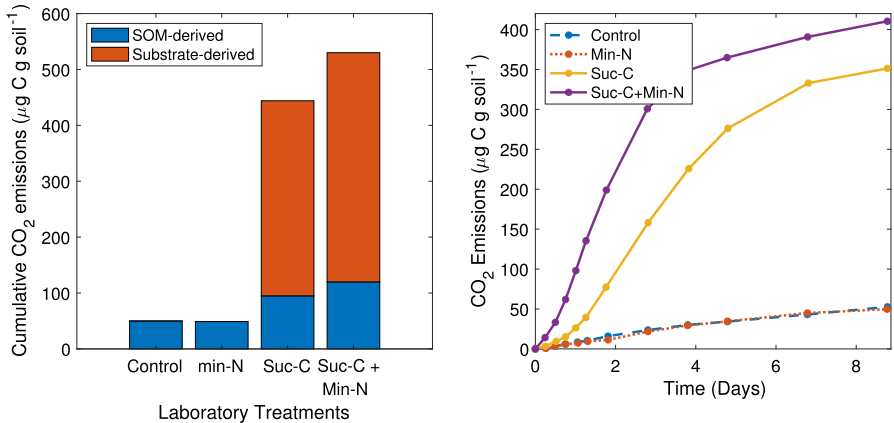
Fig. 1 Data adapted from (Chen et al. 2014). (Left panel): Cumulative CO_2 emissions from four different soil treatments in the ninth day. (Right panel): Cumulative CO_2 emissions over nine days for each experiment

treatments to soil samples previously homogenized and stored in separated jars. Part of the soil treatments was based on adding only labile *C* or *N* or a combination of both. The CO_2 emissions from SOM decomposition were directly measured, and different priming effect intensities were identified depending on the soil treatment by the ninth day.

For this work, we consider the control sample and three soil treatments: added mineral *N* (min-N), sucrose (suc-C) and min-N with suc-C. A detailed description for each treatment used in four different jars is given in Table 1. The data adapted from (Chen et al. 2014) for these treatments are provided in Fig. 1.

Mathematically speaking, different experimental treatments will correspond to different initial conditions $C(0)$, and $N(0)$ for our model. The data points represented in Fig. 1 were used to validate the model (6) with Eq. (9).

2.2 Data Fitting

The CO_2 data emissions from the laboratory experiment found in (Chen et al. 2014) were adapted using OriginPro 2020 software. The cumulative SOM degradation measured in terms of CO_2 was differentiated in the laboratory from labile *C* degradation using radioactive isotopes. Since our model tracks the cumulative CO_2 directly from
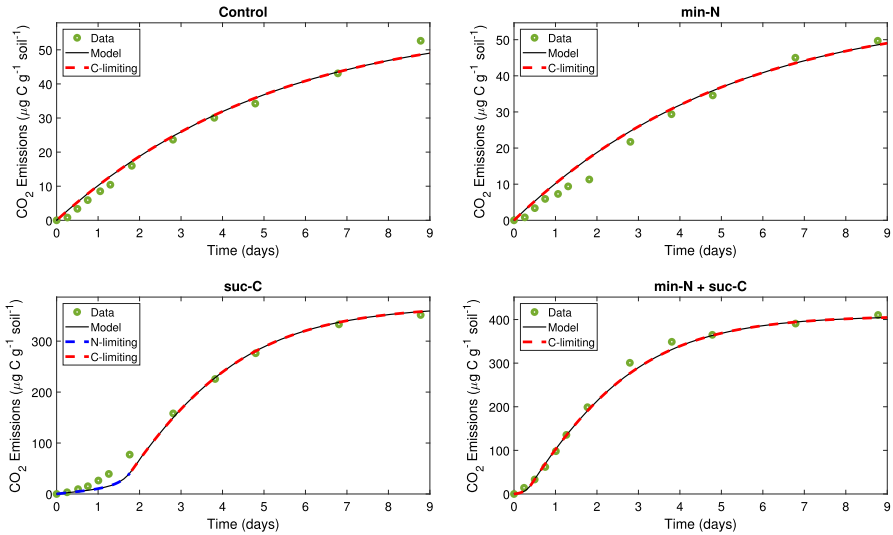
Fig. 2 Model validation using the data adapted from (Chen et al. 2014) and parameters from Tables 1, 2 and 3. Each panel represents a different soil treatment. It is shown when labile C or N limits the CO_2 emissions. The system is mostly C-limited because it is not considered an external sink of labile nutrients such as plants

microbial respiration, a discrepancy arises between the laboratory data set and the model predictions. This discrepancy leads to the unavailability of parameters for the system (1). However, some parameters are found in the literature, and the rest were fit.

We split the data into four groups corresponding to each treatment as in Table 1. Then, we simultaneously fit Eqs. (6) and (9) for each group with different initial conditions corresponding to each treatment. We predict the four data groups with fixed parameters and different initial conditions. A full description of the parameters used, and supporting references, can be found in Tables 2 and 3. For this particular case, we consider the death rate $\epsilon = 0$ given the short period of the experiment.

To avoid over-fitting, the ratio #(data points)/#(free parameters) is 4.8. The free parameters are estimated using a nonlinear regression function in MATLAB (*nlinfit*). We determine the goodness of fitness from predictions given by Eq. (9) by using the normalized mean square error (NMSE) function defined in MATLAB as

$$\text{NMSE} = 1 - \frac{\|x_0 - x_1\|^2}{\|x_0 - \overline{x_0}\|^2},\qquad(13)$$

where $\|.\|$ is the Euclidean norm, x_0 is a vector that contains data points, x_1 is the predictions from the model, and $\overline{x_0}$ is the mean of the experimental data points. The function NMSE defined in MATLAB measures the goodness of fitness predicted in the interval $(-\infty, 1]$ where the perfect fit is if the function is equal to one. The minimum value we achieved using the NMSE function was about 0.9, and the numerical simulation is shown in Fig. 2. We estimated the 95% confidence intervals using the

Table 2 List of parameters used for the numerical simulation. H.S.C stands for half-saturation constant. C.I. stands for confidence interval

Param	Definition	Value/Range	Unit	Refs.	95% C.I
μ_c	Max. growth rate for labile C	8.31	day^{-1}	Fitted	[7.35– 9.27]
μ_s	Max. growth rate for C_s	6.62	day^{-1}	Fitted	[6.21–7.04]
l	Respiration rate	3.05	day^{-1}	Fitted	[2.94–3.12]
ϵ	Microbial death rate	0/[0.1056]	day^{-1}	Smith (1982)	–
r_1	Yield constant	0.104/[0–1]	–	Fitted	[0.09–0.117]
r_2	Yield constant	0.103/[0–1]	–	Fitted	[0.067–0.14]
θ	Microorganisms N:C ratio	0.2	–	Sterner and Elser (2017)	–
θ_s	SOM decomposition N:C ratio	0.3946	–	Fitted	[0.371–0.417]
K_f	N-dependent H.S.C. for microorganisms growth	2.9	µg N g soil^{-1}	Smith (1982)	–
K_g	C-dependent H.S.C. for microorganisms growth	30	µg C g soil^{-1}	Smith (1982), Martin (1971)	–
K_{f_s}	N_s-dependent H.S.C. for microorganisms growth	1277.42	µg N g soil^{-1}	Fitted	1277.42
K_{g_s}	C_s-dependent H.S.C. for microorganisms growth	19.1164×10^3	µg C g soil^{-1}	Fitted	[19145.7–19177.7]
K_h	C-dependent H.S.C. for microorganisms strategy	474.78	µg C g soil^{-1}	Fitted	[325.22–624.33]

Table 3 Initial conditions

Initial condition	Values	Unit	Reference	95% C.I
$B(0)$	3.63	μg C g soil^{-1}	Fitted	[2.89–4.37]
$C(0)$	$\{0, 500\}$	μg C g soil^{-1}	Chen et al. (2014)	–
$N(0)$	$\{0, 110\}$	μg N g soil^{-1}	Chen et al. (2014)	–
$C_s(0)$	1.47×10^4	μg C g soil^{-1}	Chen et al. (2014)	–
$N_s(0)$	980	μg N g soil^{-1}	Chen et al. (2014)	–

MATLAB function (*nlparci*) and the coefficient estimates, residuals and the estimated covariance matrix from *nlinfit*.

The data fitting reveals that SOM decomposition dynamics are governed primarily by C_s transients for this particular data set. The degradation efficiency for the nutrient uptake in SOM (K_{f_s}) determines if C_s or N_s dynamics govern SOM decomposition. If $K_{f_s} < K_{g_s} N_s(t)/C_s(t)$, for some t, then SOM dynamics are governed by C_s; otherwise, it will be governed by N_s. By choosing $K_{f_s} \approx K_{g_s} N_s(0)/C_s(0)$, we discard the possibility that SOM decomposition is governed by C_s limitation only.

3 Numerical Simulations

We validate our model by comparing the predictions of CO_2 from the model to the adapted laboratory data set. However, the model predictions of the degradation of SOM differ somewhat from reality. The first panel in Fig. 3 shows the cumulative decomposed SOM on the ninth day of each experiment. The numerical simulation for SOM decomposition is at least consistent with the experiment in Chen et al. (2014), i.e., a combination of added labile substrates promotes a higher decomposition rate of SOM rather than using only N and C separately.

Our simulations show that the system is C-limited predominantly for all treatments, except when labile C is added. This is because we are not assuming other external sinks of labile nutrients, such as plants' N uptake for biomass formation. Adding only labile N will not increase the SOM decomposition, and microbial N mining mechanism strength remains weak, since there is no labile C to utilize. Adding labile C increases the microbial N mining mechanism strength; consequently, more nutrients from SOM are released, increasing microbial biomass production. Adding labile C and N will increase the SOM decomposition at higher rates by rapidly increasing microbial biomass and activities subject to the stoichiometric decomposition mechanism (see Fig. 3).

Measuring the robustness of the model will provide insightful performance on the model's predictions on SOM decomposition as information on the sensitivity of the parameters used. The reliability of SOM dynamics predictions with respect to the availability of labile substrates can be measured, and we may track down those crucial parameters during the priming effect with a sensitivity analysis.
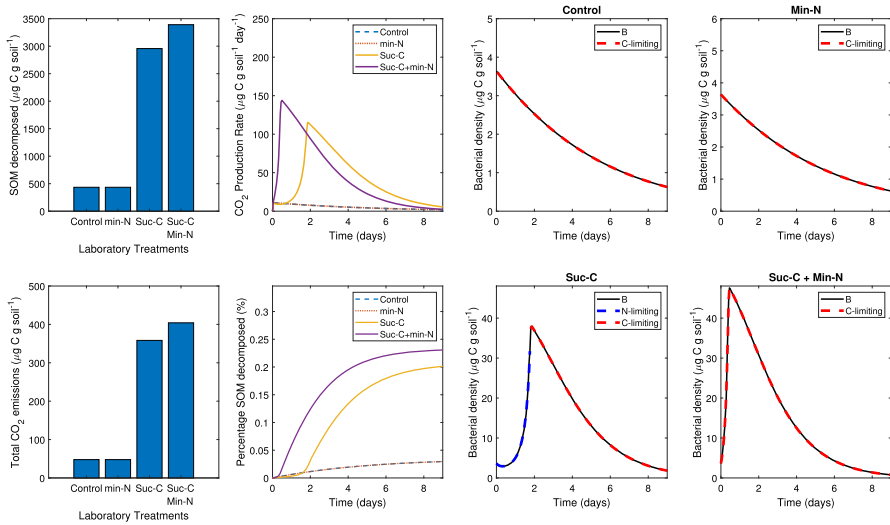
Fig. 3 Numerical simulations of the model (6) and (9) using Tables 2, 3 and 1. (First column): Cumulative SOM decomposed and CO$_2$ emissions. (Second column): CO$_2$ production and percentage of SOM decomposed with respect to time. (Third and fourth column): Simulated microorganisms biomass subject to different SOM decomposition mechanisms

3.1 Sensitivity Analysis

We perform a local sensitivity analysis to understand how significantly the parameters used in the model affect SOM decomposition. Each parameter sensitivity index can measure the relative importance of the parameters influencing SOM degradation. The definition of the normalized forward sensitivity index is

$$\gamma_p^u := \frac{\partial u}{\partial p} \times \frac{p}{u}, \tag{14}$$

where u is the variable that depends differentiably on the parameter p. A forward difference scheme is needed to compute the sensitivity index because of the absence of an explicit solution of system (6). The numerical sensitivity index is

$$\gamma_p^u = \frac{u(p + \Delta p) - u(p)}{\Delta p} \times \frac{p}{u(p)}, \tag{15}$$

where $u(p)$ refers to the variable of interest dependent on the parameter p, and Δp should be a small quantity such as 1% of the default value of p. The sensitivity index γ_p^u is a real number by which we can measure the relative importance of a parameter, and the sign of this value is the positive (or negative) relationship concerning the variable u.
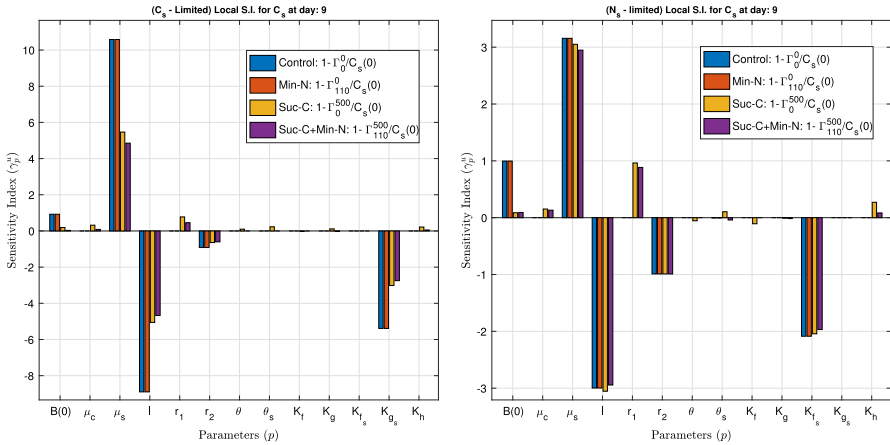
Fig. 4 Sensitivity index (S.I.) for $u = 1 - \Gamma_i^j/C_s(0)$ for $i = \{0, 100\}$ and $j = \{0, 500\}$ of SOM decomposition when different treatments are considered. (Left panel): S.I using parameters in Table 2. In this case, the system is C_s-Limited ($K_{f_s} < K_{g_s} N_s(0)/C_s(0)$). (Right panel): S.I. when the system is N_s-Limited, i.e., we choose K_{f_s} such that $K_{f_s} > K_{g_s} N_s(0)/C_s(0)$

We denote Γ_i^j as $C_s(9)$ with the parameters given in Table 2 and the initial conditions given in Table 3 but with $N(0) = i$ and $C(0) = j$. We consider the variable

$$u = 1 - \frac{\Gamma_i^j}{C_s(0)}, \tag{16}$$

to compute the sensitivity index for the percentage of SOM decomposed on the ninth day for $i = \{0, 110\}$ and $j = \{0, 500\}$ to represent the different experimental treatments. Thus, we can measure the importance of each parameter in our model for SOM decomposition predictions. The parameter's positive (negative) relationship strength depends on each soil treatment. The sensitivity analysis reveals the model's robustness and the positive (negative) strength of SOM decomposition on the ninth day of the experiment. From Fig. 4, it may be surprising that the parameter μ_s, associated with slow-growing bacteria but predominant in SOM degradation, is more beneficial to SOM conservation. Based on the data fitting, the system is primarily C_s-limited, but SOM decomposition under N_s-limitation was also investigated. We computed the sensitivity index for these two circumstances, guaranteeing the model's robustness for different scenarios.

3.2 Numerical Experiment: Impact of Exogenous Labile *C* and *N* in SOM Decomposition

The addition of a combination of labile substrates controls the strength of the priming effect and, in consequence, increased atmospheric emissions of CO_2 from soils in short periods. The addition of only labile *C* increases SOM decomposition during the laboratory experiment, and the decomposition is higher when exogenous labile *C* and
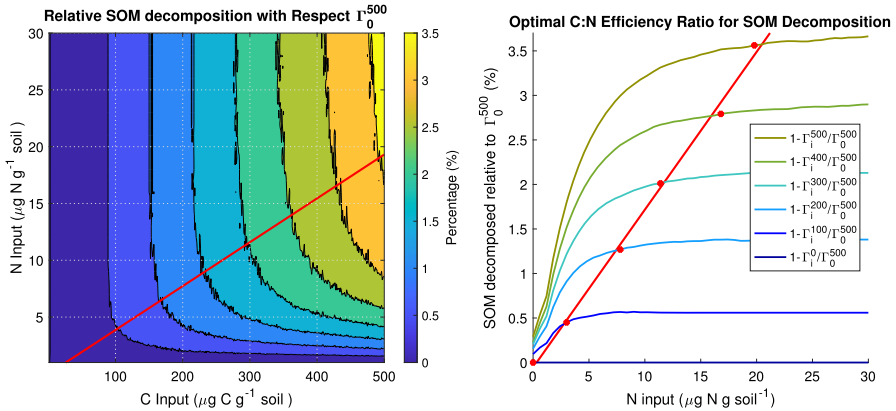
Fig. 5 Impact of adding an initial single dose of labile N and C to soils during SOM decomposition. (Left panel): Relative SOM decomposition increment when the combination of $C(0) = j$ and $N(0) = i$ is considered and compared to when only $C(0) = 500$ is added as $1 - \Gamma_i^j / \Gamma_0^{500}$. (Right panel): Different curves generated by $1 - \Gamma_i^j / \Gamma_0^{500}$ when $i = \in [0, 30]$ and $j = \{0, 100, 200, \ldots, 500\}$. The red line in both panels is given by $N(C) = C/25.83$ and represents an optimal C/N initial ratio to maximize SOM decomposition in terms of efficiency and is generated by a linear regression using the points (i, j) such that $|\Gamma_i^j - \Gamma_{30}^j| < \varepsilon \Gamma_0^{500}$ for $\varepsilon = 0.1$ (Color figure online)

N are combined. We explore numerically how the combination of a single input of $C(0) \in [0, 500]$ and $N(0) \in [0, 30]$ at $t = 0$ influences SOM decomposition.

From Fig. 5(left panel), we show the relative SOM decomposition increment when the combination of $C(0) = j$ and $N(0) = i$ is considered and compared to when only $C(0) = 500$ is added as $1 - \Gamma_i^j / \Gamma_0^{500}$ for $i \in [0, 30]$ and $j \in [0, 500]$. Furthermore, we show an optimal C/N ratio, represented by the red line in the same figure, initially required to decompose SOM efficiently, minimizing the resources of labile substrates. We also plot different curves generated by $1 - \Gamma_i^j / \Gamma_0^{500}$ on the right panel of the same figure when $i = \in [0, 30]$ and $j = \{0, 100, 200, \ldots, 500\}$. The red dots in each curve generate an optimal C/N ≈ 26 ratio to decompose SOM efficiently, and they are represented by maximum (i, j) such that $|\Gamma_i^j - \Gamma_{30}^j| < \varepsilon \Gamma_0^{500}$ for $\varepsilon = 0.1$. We choose the specified interval for $N(0) \in [0, 30]$ because adding larger labile N inputs does not change the results qualitatively, suggesting that low input of labile N may have the same potential to greatly impact SOM decomposition as high inputs of labile N.

We extend our results regarding the optimal C/N ratio inputs to maximize SOM by considering different SOM carbon-to-nutrient ratios (C_s/N_s). By fixing the total amount of carbon in SOM ($C_s(0)$), we estimate the labile C/N ratios required as initial amendments to decompose SOM efficiently in terms of the initial nutrient richness in it ($N_s(0)$). In Fig. 6, we can see that high (low) amounts of labile N will maximize SOM decomposition for nutrient-rich (nutrient-poor) soils. These results show that the C/N ratio to maximize SOM decomposition will depend on the dynamics that govern SOM decomposition, that is, when SOM is C_s or N_s limited. If SOM dynamics are strictly governed by C_s transients, then the optimal C/N ratio remains constant, but if
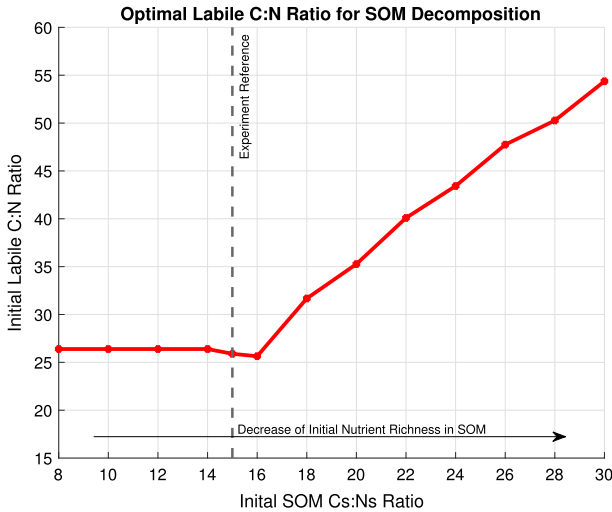
Fig. 6 Optimal initial C/N ratio to decompose SOM efficiently with respect to the SOM nutrient richness ratio. The experimental reference is $C_s(0)/N_s(0) = 15$, and the labile C/N ratio for labile substrates in the laboratory experiment was approximately 4.5. The optimal labile C/N ratio is constant for nutrient-rich soils, and it increases linearly for nutrient-poor soils
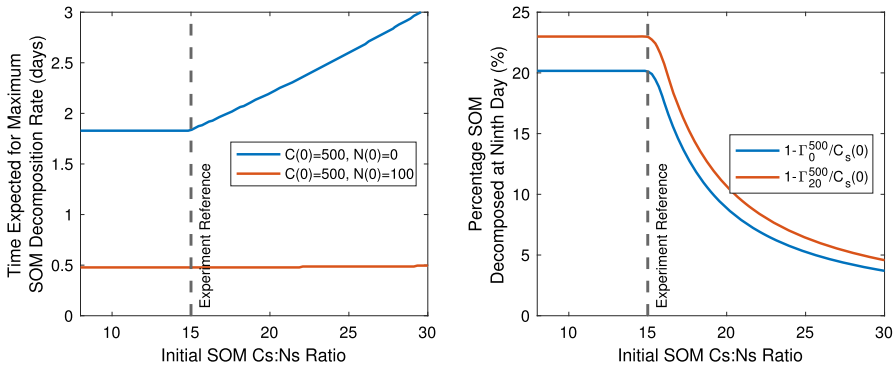

Fig. 7 (Left panel): Time expected for the priming effect to occur, i.e., when microbial communities decompose SOM at its maximum rate. (Right panel): Percentage of decomposed SOM by different treatments by the ninth day

N_s transients govern it, then the optimal C/N ratio will increase linearly with respect to the initial carbon-nutrient content in SOM.

The expected time required for microbial communities to decompose SOM at its highest rate (t_M) will depend on the initial amendments and initial C_s/N_s ratio. We compared the predicted time t_M for two different amendments. Specifically, we consider only $C(0) = 500$, $N(0) = 0$ and when $C(0) = 500$, $N(0) = 20$ as an optimized treatment. Also, we computed the percentage of SOM carbon decomposed relatively to $C_s(0)/N_s(0)$ ratios by the ninth day using the same amendments (see Fig. 7). By adding labile C and N, the t_M is constant because the stoichiometric decomposition
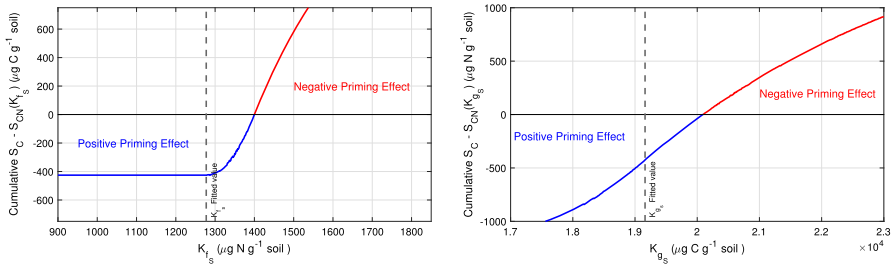
Fig. 8 Difference of cumulative decomposed SOM between soil treated with $C(0) = 500$, $N(0) = 0$ (Γ_0^{500}), and with $C(0) = 500$, $N(0) = 20$ (Γ_{20}^{500}) varying K_{f_s} (left panel) and K_{g_s} (right panel) on the ninth day. The parameters are taken as in Table 2. The initial conditions for other variables are considered as in Table 3. The model is capable to reproduce positive (negative) priming effects depending on the value for the half-saturation constant for f_s and g_s

mechanism is immediately at its highest, independent of SOM nutrient content. In contrast, adding only labile C will increase the t_M for nutrient-poor soils and remains constant for nutrient-rich soils. The microbial N mining mechanisms will predominate for larger periods in nutrient-poor soils until enough nutrients are released from SOM decomposition. The percentage of decomposed carbon in SOM at ninth day is constant for nutrient-rich soils and will decrease for nutrient-poor soils. These results show that the soil's nutrient richness determines the time and strength of the priming effect.

3.3 Numerical Experiment: Positive and Negative Priming Effect

The results from the laboratory experiments in (Chen et al. 2014) showed a positive priming effect when Suc-C and Suc-C+min-N were added to soil samples. However, there was not a significant statistical difference after adding min-N. Positive or negative priming effects, i.e., increase or reduction of SOM decomposition after adding labile substrates, respectively, have been documented when N is added into soil samples (Kuzyakov et al. 2000). For example, in Janssens et al. (2010) it is stated that nitrogen depositions reduce SOM decomposition in temperate forests.

In our model, the SOM degradation efficiency of K_{g_s} and K_{f_s} is highly related relatively to the cumulative SOM decomposition (see Fig. 4). SOM priming depends on the input of labile sources C and N, and microbial activities. However, microbial activities also rely on their ability to uptake resources from SOM. To understand how the SOM degradation efficiencies regulate the priming effect strength for two different soil treatments, we propose the following numerical experiment by considering K_{g_s} and K_{f_s} as parameters.

We define $S_C = C_s(0) - \Gamma_0^{500}$ as our numerical experiment reference, and we compute the difference with $S_{CN}(K) = C_s(0) - \Gamma_{20}^{500}$ but varying only $K = K_{f_s}$ ($K = K_{g_s}$) which is the half-saturation constant for f_s (g_s). In Fig. 8, the positive (negative) value indicates a negative (positive) priming effect concerning the different values of the half-saturation constants. We suggest that the half-saturation for recalcitrant carbon and nitrogen saturating functions in SOM should not be considered a constant

but a function of other physical properties. In this way, the system will potentially show negative priming effects even if the soils are treated with a combination of labile compounds.

4 Discussion

The CO_2 emissions derived from soils have been a subject of interest in the last years due to the potential effects of global warming. In particular, sudden increments of SOM decomposition rates in short periods derived from using labile substrates such as fertilizers have gained attention, and different mechanisms have been proposed to explain these increments over the last decades (Lal and Follett 2009; Kuzyakov et al. 2000). Recently, a laboratory experiment has supported combining the 'microbial N mining' and 'stoichiometric decomposition' mechanism to explain this natural phenomenon named the priming effect (Chen et al. 2014). Various mathematical models successfully model the priming effect without considering explicitly both mechanisms or only tracking carbon pools (Neill and Gignoux 2006; Lawrence et al. 2009). Incorporating these mechanisms, as nitrogen dynamics, is needed to increase the accordance between mathematical models and data measurements (Chen et al. 2014; Blagodatsky et al. 2010). Therefore, we proposed for the first time the inclusion of both mechanisms to explain the priming effect as carbon and nitrogen dynamics in a novel stoichiometric mathematical model.

The mathematical model in this work encompasses microbial utilization of different labile and recalcitrant carbon and nitrogen pools to predict the strength of the priming effect in soils with diverse SOM carbon and nutrient contents. Based on the laboratory data adapted to validate the model, we were required to estimate those parameters that were not available in the literature with 95% confidence. Our results predicted that the carbon dynamics in SOM principally governed the laboratory experiment results. Under this assumption and considering that the model is nutrient closed, simplifying the model by tracking only carbon dynamics in SOM would be possible. However, SOM degradation may be subject to nutrient content, and we considered that possibility in our model predictions.

We validated our results and showed model prediction robustness through a local sensitivity analysis. The laboratory experiment used abundant soil treatments in labile carbon and nitrogen to produce the priming effect. However, we predicted an optimized labile C/N ratio of approximately 26 would have the same results compared to C/N ratio of 4.54 used for the experiment. This prediction assumes that soil amendments based on only labile carbon are enough to produce the priming effect and increase by adding labile nitrogen. Furthermore, we found that the optimized ratio of labile substrates to decompose SOM efficiently remained constant for nutrient-rich soils and increased for nutrient-poor soils. This result is comparable with the prediction in (Fontaine et al. 2003), which predicted that nutrient-poor soils are more often subject to the priming effect than nutrient-rich soils. Our results showed that less labile nitrogen input is needed to maximize SOM decomposition in nutrient-poor soils. Studying how nutrient richness in soils affects the model predictions, we found that in nutrient-rich soils, the priming effect is likely to happen in short periods. Still, depending on the soil

treatment, it may be delayed and weakened in nutrient-poor soils. Finally, given the sensitivity analysis, we determined that the SOM degradation efficiency determines the increase or reduction of the priming effect on this model, which can be correlated with other physical properties like temperature (Eppley et al. 1969), for example.

This model still has limitations. First, the assumption for the function that modulates SOM decomposition mechanisms is heuristic, and predictions could improve by using mechanistic fundamentals. Second, the CO_2 emissions, when only carbon is used as a soil treatment, still present inaccuracies at the beginning of the simulation. The heuristic function that modulates both mechanisms may still be improved to produce better results without compromising its use to modulate the mechanisms behind the priming effect. The model also suggests that the SOM degradation efficiencies should be considered parameters, not constants, for general situations. Otherwise, the model may not accurately represent the negative priming effect. Another limitation is that the model is robust for short periods and is based on the assumption that it is nutrient closed. However, these issues will open more research directions, for example, considering the nutrient uptake by plants, SOM decomposition for larger periods and continuous or periodic inputs of labile substrates.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

Alijani MK, Wang H, Elser JJ (2015) Modeling the bacterial contribution to planktonic community respiration in the regulation of solar energy and nutrient availability. Ecol Complex 23:25–33

Beeckman F, Motte H, Beeckman T (2018) Nitrification in agricultural soils: impact, actors and mitigation. Current Opin Biotechnol 50:166–173

Bhatti J, Tarnocai C (2009) Influence of climate and land use change on carbon in agriculture, forest, and peatland ecosystems across Canada. Soil Carbon Sequestration Greenh Effect 57:47–70

Blagodatskaya E, Kuzyakov Y (2008) Mechanisms of real and apparent priming effects and their dependence on soil microbial biomass and community structure: critical review. Biol Fertil Soils 45(2):115–131

Blagodatskaya E, Blagodatsky SA, Anderson TH et al (2007) Priming effects in chernozem induced by glucose and n in relation to microbial growth strategies. Appl Soil Ecol 37(1–2):95–105

Blagodatsky S, Blagodatskaya E, Yuyukina T et al (2010) Model of apparent and real priming effects: linking microbial activity with soil organic matter decomposition. Soil Biol Biochem 42(8):1275–1283

Chen R, Senbayram M, Blagodatsky S et al (2014) Soil C and N availability determine the priming effect: microbial N mining and stoichiometric decomposition theories. Global Change Biol 20(7):2356–2367

Craine JM, Morrow C, Fierer N (2007) Microbial nitrogen limitation increases decomposition. Ecology 88(8):2105–2113

Drake JE, Darby B, Giasson MA et al (2013) Stoichiometry constrains microbial response to root exudation-insights from a model and a field experiment in a temperate forest. Biogeosciences 10(2):821–838

Eppley RW, Rogers JN, McCarthy JJ (1969) Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton 1. Limnol Oceanogr 14(6):912–920

Falkowski P, Scholes R, Boyle E et al (2000) The global carbon cycle: a test of our knowledge of earth as a system. Science 290(5490):291–296

Fontaine S, Mariotti A, Abbadie L (2003) The priming effect of organic matter: a question of microbial competition? Soil Biol Biochem 35(6):837–843

Fontaine S, Hénault C, Aamor A et al (2011) Fungi mediate long term sequestration of carbon and nitrogen in soil through their priming effect. Soil Biol Biochem 43(1):86–96

Hessen DO, Ågren GI, Anderson TR et al (2004) Carbon sequestration in ecosystems: the role of stoichiometry. Ecology 85(5):1179–1192

Janssens I, Dieleman W, Luyssaert S et al (2010) Reduction of forest soil respiration in response to nitrogen deposition. Nature Geosci 3(5):315–322

Kong JD, Salceanu P, Wang H (2018) A stoichiometric organic matter decomposition model in a chemostat culture. J Math Biol 76(3):609–644

Kuzyakov Y (2010) Priming effects: interactions between living and dead organic matter. Soil Biol Biochem 42(9):1363–1371

Kuzyakov Y, Friedel J, Stahr K (2000) Review of mechanisms and quantification of priming effects. Soil Biol Biochem 32(11–12):1485–1498

Lal R, Follett RF (2009) Soil carbon sequestration and the greenhouse effect, vol 57. ASA-CSSA-SSSA

Lawrence CR, Neff JC, Schimel JP (2009) Does adding microbial mechanisms of decomposition improve soil organic matter models? A comparison of four models using data from a pulsed rewetting experiment. Soil Biol Biochem 41(9):1923–1934

Manlay RJ, Feller C, Swift M (2007) Historical evolution of soil organic matter concepts and their relationships with the fertility and sustainability of cropping systems. Agric Ecosyst Environ 119(3–4):217–233

Martin JP (1971) Decomposition and binding action of polysaccharides in soil. Soil Biol Biochem 3(1):33–41

Moorhead DL, Sinsabaugh RL (2006) A theoretical model of litter decay and microbial interaction. Ecol Monogr 76(2):151–174

Neill C, Gignoux J (2006) Soil organic matter decomposition driven by microbial growth: a simple model for a complex network of interactions. Soil Biol Biochem 38(4):803–811

Smith OL (1982) Soil microbiology: a model of decomposition and nutrient cycling. CRC Press, Inc., Boca Raton

Sterner RW, Elser JJ (2017) Ecological stoichiometry. Princeton University Press, Princeton

Stotzky G (2000) Soil Biochemistry. In: Books in soils, plants, and the environment. CRC Press, 200, https://books.google.ca/books?id=VI9N7b16CRoC

Sylvia DM, Fuhrmann JJ, Hartel PG, et al (2005) Principles and applications of soil microbiology. QR111 S674 2005, Pearson

Tate RL (1995) Soil microbiology. Wiley, New York

Wang H, Jiang L, Weitz JS (2009) Bacterivorous grazers facilitate organic matter decomposition: a stoichiometric modeling approach. FEMS Microbiol Ecol 69(2):170–179

Wang H, Sterner RW, Elser JJ (2012) On the strict homeostasis assumption in ecological stoichiometry. Ecol Modell 243:81–88

Wang H, Lu Z, Raghavan A (2018) Weak dynamical threshold for the strict homeostasis assumption in ecological stoichiometry. Ecol Modell 384:233–240