LETTER

Size and functional diversity of microbe populations control plant persistence and long-term soil carbon accumulation

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Abstract

Soil organic matter (SOM) models are based on the equation $dC/dt = -kC$ which states that the decomposition rate of a particular carbon (C) pool is proportional to the size of the pool and the decomposition constant k. However, this equation does not adequately describe the decomposition of recalcitrant SOM compounds. We present an alternative theory of SOM dynamics in which SOM decay rate is controlled by the size and the diversity of microbe populations and by the supply of energy-rich litter compounds. We show that the SOM pool does not necessarily reach equilibrium and may increase continuously, which explains how SOM can accumulate over thousands of years. However, the simulated SOM accumulation involves the sequestration of available nutrients. How can plants persist? This question is explored with two models that couple the C cycle with a limiting nutrient. The first model considers a single type of microbe whereas the second includes two functional types in competition for energy and nutrient acquisition. The condition for plant persistence is the presence of these two competing microbial types.

INTRODUCTION

Soil organic matter (SOM) represents the major carbon reservoir of the biosphere–atmosphere system and the main nutrient source for plant growth (Falkowski *et al*. 2000). Consequently, predicting carbon (C) and nitrogen (N) cycling through SOM is crucial in order to predict global changes and to allow for the adoption of alternative agricultural practices that enable a decrease in the use of mineral fertilizers. Modelling SOM dynamics is not a novelty in soil science and many models already exist (Jenny 1941; McGill 1996). However, whilst these models provide accurate simulations of SOM dynamics for a variety of land uses (Smith *et al*. 1997), some empirical results on long-term SOM dynamics in natural ecosystems remains unexplained. For example, it is generally thought that the soil sink capacity is limited and that old non-disturbed soils should have reached equilibrium in terms of their C balance (Lal 2004). Paradoxically, there has been a steady C accumulation in the soils of many ecosystems over millennia (Syers *et al*. 1970; Schlesinger 1990). Moreover, the mean age of SOM is of the order of decades at soil surface (> 0.15 m) whereas it may be thousands of years old in deeper soil horizons (< 0.5 m) (Martel & Paul 1974; Rumpel *et al*. 2002). The only way to explain this result using current models would be to consider an extreme change in the chemical composition of SOM along soil profiles. However, to date no analysis of the chemical and physical composition of SOM along soil profiles reveals such an extreme change (Rumpel *et al*. 2002; Krull & Skjemstad 2003). These intriguing results stress the need for a better knowledge of the mechanisms involved in SOM mineralization.

Soil organic matter is the result of the long-term accumulation in soils of biochemically recalcitrant C compounds and more or less decomposable compounds that are physically sequestered by soil minerals (Torn *et al*. 1997; Jastrow & Miller 1998). In artificial culture, the addition of energy-rich substrates enables some microbes to

actively degrade these recalcitrant C compounds with their extracellular enzymes (Blondeau 1989). However, energy-rich substrates are scarce in natural soil. As a result, the decomposition of SOM should be slow because the acquisition of energy from such substrates is low and cannot sustain microbial growth (Paul & Clark 1989). This lack of microbial growth probably explains why microbial C does not exceed 1–2% of the total soil C (Paul & Clark 1989).

Given this energy limitation in soils, fresh organic matter (FOM) like plant litter may act as a source of energy-rich substrates and increase the rate of SOM mineralization (Löhnis 1926). This acceleration of SOM mineralization by the supply of FOM, the so-called 'priming effect of organic matter' (*sensu* Bingeman *et al.* 1953), has been difficult to demonstrate experimentally until recently (Wu *et al.* 1993; Fontaine *et al.* 2004a,b). Moreover, the mechanisms involved in the priming effect are not fully understood (Kuzyakov *et al.* 2000; Fontaine *et al.* 2003). The supply of FOM is thought to stimulate SOM mineralization through a general stimulation of microbial activities. The delivery of energy-rich compounds such as glucose or fructose, however, has no effect on SOM mineralization although it strongly stimulates microbial growth and respiration (Dalenberg & Jager 1989; Wu *et al.* 1993). This lack of predictive understanding explains why current models do not include the priming effect (McGill 1996). However, the priming effect has important consequences on SOM dynamics. The supply of FOM can increase the mineralization of SOM by 12–400% depending on the FOM characteristics, the addition rate and the soil mineral nutrient status (Wu *et al.* 1993; Cheng *et al.* 2003; Fontaine *et al.* 2004b). Increased rates of SOM mineralization persist in soil for several months after the complete decomposition of FOM, which leads with time to important C losses (Fontaine *et al.* 2004a). Such priming may even induce a negative C balance, i.e. the supply of C decreases the total soil C content (Fontaine *et al.* 2004b). Consequently, model predictions may differ radically if the priming effect is taken into account.

Recent advances in our understanding of the mechanisms involved in the priming effect provide guidelines for modelling this phenomena. These studies provide evidence that the priming effect depends both on the supply of energy to decomposers, and also on competition between microbial functional types (Fontaine *et al.* 2003, 2004a,b). The supply of FOM not only stimulates the decomposers of SOM, but also stimulates FOM-specialized decomposers. These FOM decomposers, commonly classified as *r*-strategists, grow quickly and specifically consume FOM (e.g. Lemoigne *et al.* 1951; Pianka 1970). Thus, there are two microbial functional types that compete for FOM, one degrading exclusively FOM (the *r*-strategy FOM decomposers) and the other, while being able to breakdown FOM, nevertheless mainly lives on SOM (the *K*-strategy SOM decomposers). Based on this competition for resources, it should be possible to predict the impact of FOM and soil mineral nutrients on the intensity of the priming effect (Fontaine *et al.* 2003).

In this paper, we explore how including the priming effect in current SOM models could result in qualitatively different predictions about C and N cycling. To this end, we present a theory of SOM dynamics in which SOM decay rate is controlled by the size and diversity of microbe populations and by the supply of FOM. Although some current models already separate microbial biomass into two or more functional types these biomasses are mostly treated as organic matter pools and are not considered to control the SOM decay (Jenkinson & Rayner 1977; McGill 1996). Our approach uses a series of mathematical models of increasing complexity to find the minimal set of mechanisms required to account for empirical evidence of the priming effect, long-term SOM dynamics and plant–microbe coexistence in ecosystems.

We first present two simple C-based models including a single type of primary decomposers (the SOM decomposers): a decomposition model describing the dynamics of the decomposition-microbial growth system (model 1); a model of SOM dynamics that further includes SOM synthesis (model 2). We show that these models can predict the lack of SOM decomposition in deep soil and the steady accumulation of SOM in ecosystems. However, the simulated SOM accumulation involves the sequestration of nutrients, which is likely to lead to a nutrient shortage threatening plant persistence. This being the case, how can plants persist? This question was explored with two stoichiometrically explicit models that couple the C cycle (described previously) with a limiting nutrient. We use N as an example of a limiting nutrient for plants but our models may be applicable to other nutrients such as phosphorus (e.g. Harrington *et al.* 2001). The models do not explicitly represent the plant compartment but we state that plant persistence implies that the N input to soil owing to plant FOM losses (plant litters and excretions) must be compensated by an equivalent output of N from the soil mineral pool. Otherwise, plants could not compensate their N loss and would disappear (Tilman 1990). The first C–N model (model 3) considers a single type of decomposers whereas the final model includes two functional types of decomposers: the SOM decomposers and the FOM decomposers (model 4). We analyse these models and show that the condition for plant persistence is the presence of these two microbial types.

THE MODELS

Definitions of variables and parameters are summarized in Table 1.

Table 1 Variables and parameters of the four models

Symbol	Definition	Dimension
Model 1		
C_s	Carbon stock in soil organic matter (SOM)	Quantity of carbon
C_{ds}	Carbon stock in SOM decomposers	Quantity of carbon
A	Decomposers consumption rate of SOM	Time^{-1}
r	Fraction of decomposer biomass released as CO_2	Time^{-1}
Φ_l	Fresh organic matter (FOM) carbon flux	(Quantity of carbon) (time)$^{-1}$
Idem for model 2, and		
s	Decomposers production rate of SOM	Time^{-1}
Idem for model 3, and		
C_f	Carbon stock in FOM	Quantity of carbon
α	Nitrogen : carbon ratio in SOM and in decomposers	Dimensionless
β	Nitrogen : carbon ratio in FOM	Dimensionless
k	FOM decomposition rate under substrate limitation	Time^{-1}
i	Rate of mineral N diffusion in soil	Time^{-1}
Φ_d	Carbon flux associated with the decomposition of FOM by SOM decomposers	(Quantity of carbon) (time)$^{-1}$
Φ_{IMS}	Nitrogen immobilization-mineralization flux induced by SOM decomposers	(Quantity of nitrogen) (time)$^{-1}$
Φ_i	Nitrogen that flows into the ecosystem	(Quantity of nitrogen) (time)$^{-1}$
Φ_o	Nitrogen that flows out of the ecosystem	(Quantity of nitrogen) (time)$^{-1}$
Φ_{up}	Nitrogen flux associated with the nitrogen uptake by the plant cover	(Quantity of nitrogen) (time)$^{-1}$
Idem for model 4, except k is deleted, and		
C_{df}	Carbon stock in FOM decomposers	Quantity of carbon
y	SOM-decomposer consumption rate of FOM under substrate limitation	Time^{-1}
u	FOM-decomposer consumption rate of FOM under substrate limitation	Time^{-1}
Φ_f	Carbon flux associated with the decomposition of FOM by FOM decomposers	(Quantity of carbon) (time)$^{-1}$
Φ_{IMf}	Nitrogen immobilization–mineralization flux induced by FOM decomposers	(Quantity of carbon) (time)$^{-1}$

The model of SOM decomposition: model 1

Traditional SOM models are based on the first-order kinetics $dC/dt = -kC$ which states that the decomposition rate of a particular C pool is proportional to the size of the pool and the decomposition constant k (McGill 1996). Although this formalism seems relevant for easily degradable litter compounds it is not well suited to describe the decomposition of recalcitrant SOM compounds because in this latter case the decomposition rate is limited by the quantity of 'enzymes' and not by the quantity of 'substrates'. Indeed, a substantial amount of SOM is available in soils but the low quality of this organic matter restricts microbial growth and enzymatic activities (Paul & Clark 1989, but see also Schimel & Weintraub 2003). This limitation by the amount of 'enzymes' is confirmed by experiments which indicates a high acceleration of SOM mineralization after addition of FOM (Wu *et al.* 1993; Fontaine *et al.* 2004a,b). As SOM decomposition is limited by the amount of 'enzymes', the overproduction of enzymes by stimulated decomposers accelerates SOM decomposition.

Based on this limitation by the amount of 'enzymes', we constructed the simplest model of SOM decomposition (Fig. 1a). Soil organic C (C_s) is degraded by the

decomposers (C_{ds}) that are supplied by a flux of FOM from the non-modelled plant compartment (Φ_l). Decomposers respire and die, which releases CO_2 (r). The rate of SOM decomposition is assumed to be proportional to decomposer biomass. Thus, the supply of FOM increases the decomposer biomass and the rate of SOM decomposition, which is the priming effect. The model equations read as follows:

$$\frac{dC_s}{dt} = -AC_{ds}, \tag{1}$$

$$\frac{dC_{ds}}{dt} = (A - r)C_{ds} + \Phi_l, \tag{2}$$

where A is the rate of SOM consumption by the decomposers.

The model of SOM dynamics: model 2

Recalcitrant compounds of plant and microbial origin are released in soil by soil microbes (Jastrow & Miller 1998). These compounds accumulate in soil, which leads to the formation of SOM in the long term. SOM may have plant or microbial origins but this distinction does not change the
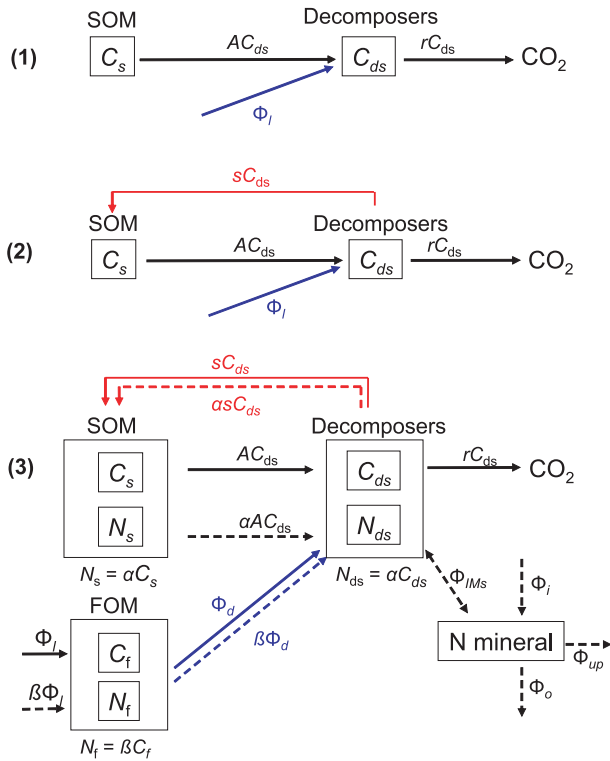
Figure 1 Flow diagram of the decomposition model (model 1), the soil organic matter dynamics model (model 2) and the carbon and nitrogen coupled model (model 3). The three models assume one single type of decomposer. The arrows represent the carbon (continuous arrows) and nitrogen (dashed arrows) flows between compartments.

behaviour of the model. We ignore this complication and assume that the production rate of SOM (s) is proportional to the decomposer biomass. The model equations read as follows (Fig. 1b):

$$\frac{dC_s}{dt} = (s - A)C_{ds}, \tag{3}$$

$$\frac{dC_{ds}}{dt} = (A - r - s)C_{ds} + \Phi_l, \tag{4}$$

where $s + r$ is the turnover rate of decomposers.

The C–N model of SOM dynamics with a single type of decomposer: model 3

As SOM contains N (Himes 1997), SOM accumulation in soil involves the sequestration of N that is usually scarce in soils. This could decrease N availability for plants, threaten plant persistence in ecosystems and also alter the functioning of decomposers. Indeed, the C : N ratio of FOM (plant litter) is larger than that of decomposers (Ågren & Bosatta 1996). Both because of this mismatch and because of

decomposer respiration, the maintenance of decomposer C : N ratio can lead either to the uptake of mineral N in soil solution by the decomposers (the immobilization process) or to the release of mineral N (the mineralization process) (Ågren & Bosatta 1996). In the first case, N availability in soils can be too low to allow the potential growth of decomposers: decomposers are N-limited and FOM decomposition is reduced (Recous et al. 1995). Thus, stocks and fluxes in soils depend on mass-balance constrain for C and N (Elser et al. 1996; Daufresne & Loreau 2001). Here, we explore how taking into account the co-limitation of microbes by either C or N in a stoichiometric (Elser et al. 1996) version of the previous model changes the predictions about SOM dynamics. We also test whether this third model allows plant persistence in ecosystems, i.e. whether N input to soil through FOM can be compensated for by an equivalent output of N from the soil mineral pool.

The model is made up of three carbon compartments coupled with three nitrogen compartments with constant C : N ratios, plus a compartment for soil mineral N (Fig. 1c). For the readability of equations, we express the C : N ratios as N : C ratios. In comparison with the previous model, the FOM compartment is taken into account as FOM is not necessarily degraded by the decomposers and may accumulate when mineral N is scarce. The biomass of decomposers and the SOM pool are assumed to have the same and constant N : C ratio (α) (Stevenson 1982; Himes 1997; Martens et al. 2003). In fact, the N : C ratio of decomposers is slightly higher than that of SOM but this assumption does not change the general behaviour of the model and simplifies the readability of equations. The N : C ratio of FOM (β) is constant and lower than that of decomposers (α). Uptake and release of mineral N from the decomposers are assumed to be controlled only by decomposer homeostasis alone.

Inputs and outputs of mineral N into the system are assumed to be constant. Φ_i and Φ_o represent the amount of N that flows into (atmospheric N deposition, symbiotic N fixation) and out of (N leaching, denitrification) the ecosystem, respectively, and Φ_{up} represents the N uptake by the plant cover.

Because of the strict C and N coupling in the compartments and fluxes, the dynamic equations for the model can be reduced to four independent variables, the stocks of either C or N in the decomposers, FOM, SOM and the mineral N pool. As our first two models are C based, we have chosen the C stocks to measure the organic pools:

$$\frac{dC_s}{dt} = (s - A)C_{ds}, \tag{3}$$

$$\frac{dC_f}{dt} = \Phi_l - \Phi_d, \tag{5}$$

$$\frac{dC_{ds}}{dt} = (A - s - r)C_{ds} + \Phi_d, \tag{6}$$

$$\frac{dN}{dt} = \Phi_i - \Phi_o - \Phi_{up} + \Phi_{IMs}, \tag{7}$$

where C_f, Φ_d and Φ_{IMs}, respectively, are the amount of C contained in the FOM compartment, the FOM-carbon decomposition flux, and the N immobilization–mineralization flux induced by the maintenance of the C : N ratio of SOM decomposers.

The immobilization–mineralization flux Φ_{IMs} can be determined as the difference between the organic N available for the decomposers and the total N required for the maintenance of the decomposer C : N ratio (Fig. 1c):

$$\Phi_{IMs} = \alpha A C_{ds} + \beta \Phi_d - \alpha s C_{ds} - \alpha(A C_{ds} + \Phi_d - s C_{ds} - r C_{ds}),$$

$$\Phi_{IMs} = \alpha r C_{ds} + (\beta - \alpha)\Phi_d. \tag{8}$$

The flux Φ_{IMS} is negative when the decomposers immobilize N and positive when the decomposers mineralize N.

In contrast to SOM, energy-rich FOM compounds sustain microbial growth and are quickly decomposed when N is not limiting so that FOM decomposition and decomposer growth are both limited by the amount of 'substrate' (Paul & Clark 1989). Such C limitation probably explains why the $dC/dt = -kC$ function adequately describes the decomposition of FOM. Thus, the decomposers can be either carbon- or nitrogen-limited.

Under C limitation, the decomposition flux Φ_d is expressed by the traditional function, kC_f, where k is the rate of FOM decomposition under substrate limitation (N in excess). Under N limitation, the decomposition flux Φ_d is limited by the immobilization flux. In this case, the immobilization flux $\Phi_{IMS} = -iN$, where i is the rate of mineral N diffusion in soil. Thus, according to eqn 8 the decomposition flux Φ_d can be expressed as

$$\frac{iN + \alpha r C_{ds}}{\alpha - \beta}$$

when SOM decomposers are N-limited.

Liebig's law of the minimum, expressed in its simplest way (Grover 1997), determines whether SOM decomposers are C- or N-limited:

$$\Phi_d = Min\left[\frac{iN + \alpha r C_{ds}}{\alpha - \beta}, kC_f\right]. \tag{9}$$

The C–N model of SOM dynamics, two decomposer types: model 4

Because the previous model does not allow plant-decomposer coexistence (see the Results section), a second type of

decomposer has been added (Fig. 2). Two populations of microbes are thus competing for FOM and mineral N, one degrading exclusively FOM (FOM decomposers) and the other degrading FOM and SOM (SOM decomposers) (Fontaine *et al.* 2003, 2004a,b). In all other respects, FOM decomposers are similar to SOM decomposers in terms of functioning: the two decomposer types have the same N : C ratio, α, rate of CO_2 production, r, rate of SOM production, s. The model equations read as follows:

$$\frac{dC_s}{dt} = (s - A)C_{ds} + sC_{df}, \tag{10}$$

$$\frac{dC_f}{dt} = \Phi_l - \Phi_d - \Phi_f, \tag{11}$$

$$\frac{dC_{ds}}{dt} = (A - s - r)C_{ds} + \Phi_d, \tag{6}$$

$$\frac{dC_{df}}{dt} = \Phi_f - (s + r)C_{df}, \tag{12}$$

$$\frac{dN}{dt} = \Phi_i - \Phi_o - \Phi_{up} + \Phi_{IMS} + \Phi_{IMf}, \tag{13}$$

with

$$\Phi_{IMS} = \alpha r C_{ds} + (\beta - \alpha)\Phi_d,$$

$$\Phi_{IMf} = \alpha r C_{df} + (\beta - \alpha)\Phi_f, \tag{14}$$

where C_{df} is the C of FOM decomposers, Φ_f the FOM-carbon decomposition flux and Φ_{IMf} the N immobilization–mineralization flux induced by FOM decomposers.

Liebig's law of the minimum determines whether the two decomposer types are C- or N-limited:

$$\Phi_d = Min\left[\frac{iN + \alpha r C_{ds}}{\alpha - \beta}, yC_f\right],$$

$$\Phi_f = Min\left[\frac{iN + \alpha r C_{df}}{\alpha - \beta}, uC_f\right], \tag{15}$$

where y is the rate of FOM consumption by SOM decomposers and u the rate of FOM consumption by FOM decomposers under substrate limitation (N in excess). Thus, $y + u$ corresponds to the total rate of FOM decomposition under substrate limitation (k in the previous model 3).

RESULTS

The systems of differential equations defining the four models were solved to determine the size of the different compartments at equilibrium. Some compartments actually reach equilibrium, others increase or decrease according to the constant rates that can be computed.
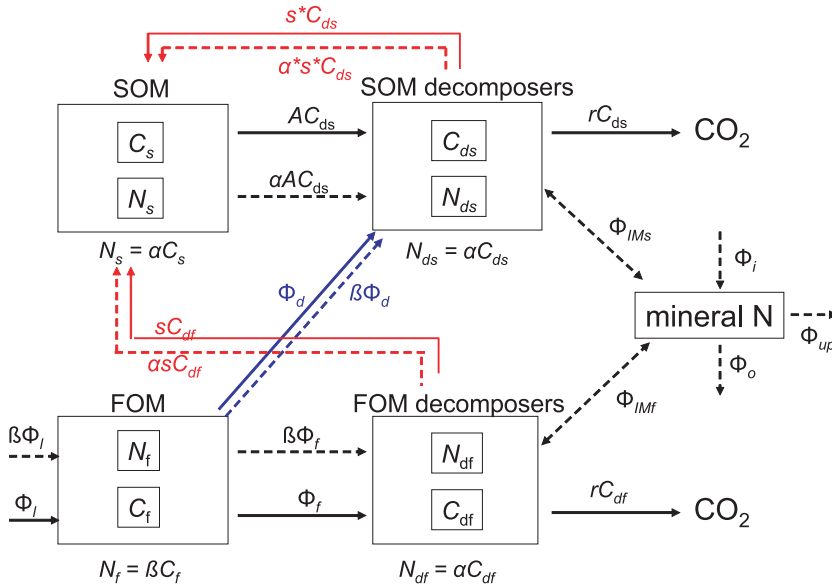
Figure 2 Flow diagram of the carbon and nitrogen model of soil organic matter dynamics, two decomposer types (model 4).

Model 1

The decomposer biomass at equilibrium is obtained by setting eqn 2 to 0

$$C_{ds}^* = \frac{\Phi_l}{r - A}. \tag{16}$$

In this case, the rate of SOM decomposition can be determined as

$$\left(\frac{dC_s}{dt}\right)^* = -AC_{ds}^* = -\frac{A}{r - A}\Phi_l. \tag{17}$$

The equilibrium value of decomposer biomass must be positive, which implies $A < r$ (eqn 16). This means that decomposers attain equilibrium only if the consumption of SOM by the decomposers does not compensate for their turnover rate. If this condition is not fulfilled, the biomass of decomposers and SOM decomposition rate continuously increase until SOM exhaustion. Moreover, as decomposers cannot use SOM as their sole source of energy, the long-term maintenance of decomposers and SOM decomposition hinge on the supply of FOM (eqns 16 and 17). Without a flux of FOM the decomposer biomass drops to 0 and SOM mineralization stops. Such a lack of decomposition is known to occur in deep soil horizons despite the availability of SOM (Martel & Paul 1974; Rumpel *et al.* 2002) and has been shown for several soils incubated for 20 years without FOM (Wadman & de Hann 1997).

Model 2

At equilibrium (eqn 3)

$$C_{ds}^* = \frac{\Phi_l}{s + r - A} \tag{18}$$

and

$$\left(\frac{dC_s}{dt}\right)^* = (s - A)C_{ds}^* = (s - A)\frac{\Phi_l}{s + r - A}. \tag{19}$$

As in the previous model, the long-term maintenance of SOM decomposition depends on the supply of FOM (eqn 18).

The SOM pool does not reach equilibrium unless $s = A$ or $\Phi_l = 0$ (eqn 19). In this specific case, the SOM pool at equilibrium (C_s^*) depends on the initial conditions used. In general although, the SOM pool continuously increases or decreases depending on whether $s - A$ is positive or negative. The values of s and A may depend on many factors affecting microbe functioning (temperature, soil moisture and mineralogy) but the energy content of FOM is likely to be the most important factor. For example, FOM with a high lignin content should have low A value relative to s. In any case, if decomposers are supplied with FOM ($\Phi_l > 0$) and if the production of recalcitrant SOM compounds is higher than the consumption of these compounds by the decomposers ($s - A > 0$), the SOM pool increases constantly without reaching equilibrium. This is consistent with the steady C accumulation in soils of many ecosystems over millennia (Syers *et al.* 1970; Schlesinger 1990).

Model 3

Here, we test whether the model allows for plant persistence in ecosystems, that is, whether the N input to soil via FOM is compensated for by an equivalent output of N from the soil mineral pool ($\beta\Phi_l - \Phi_{up} = 0$).

When decomposers are C-limited, the biomass of decomposers (C_{ds}) and the FOM pool (C_f) reach equilibrium

$$C_{ds}^* = \frac{\Phi_l}{s + r - A}$$
$$C_f^* = \frac{\Phi_l}{k}. \tag{20}$$

At this equilibrium, changes in the SOM pool and the mineral N pool follow constant rates:

$$\left(\frac{dC_s}{dt}\right)^* = (s - A)C_{ds}^* = (s - A)\frac{\Phi_l}{s + r - A},$$

$$\left(\frac{dN}{dt}\right)^* = \Phi_i - \Phi_o - \Phi_{up} + \beta\Phi_l - \alpha(s - A)\frac{\Phi_l}{s + r - A}. \tag{21}$$

Taking the condition of plant persistence ($\beta\Phi_l - \Phi_{up} = 0$) into account, the change in mineral N pool can be determined as

$$\left(\frac{dN}{dt}\right)^* = \Phi_i - \Phi_o - \alpha(s - A)\frac{\Phi_l}{s + r - A}. \tag{22}$$

As in the previous model, the SOM pool does not reach equilibrium unless $s = A$ or $\Phi_l = 0$ (eqn 21). It is also clear that any change in the SOM compartment affects the mineral N compartment because of sequestration of N in SOM (eqns 21 and 22). If we consider in eqns 21 and 22 that the SOM compartment continuously increases ($s > A$ and $\Phi_l > 0$) and that the net N supply to the ecosystem ($\Phi_i - \Phi_o$) is very low (Vitousek & Howarth 1991), then the N mineral pool decreases constantly. Thus, when decomposers are C-limited, a constant accumulation of SOM leads to the exhaustion of soil mineral N and to plant disappearance.

When decomposers are limited by N, the biomass of decomposers (C_{ds}) and the mineral N pool (N) reach the equilibrium

$$C_{ds}^* = \frac{iN*}{\alpha(s - A) - \beta(s + r - A)}$$
$$N* = \frac{\Phi_i - \Phi_o - \Phi_{up}}{i}. \tag{23}$$

At this equilibrium SOM and FOM dynamics are determined by the following constant rates

$$\left(\frac{dC_s}{dt}\right)^* = \frac{\Phi_i - \Phi_o - \Phi_{up}}{\alpha(s - A) - \beta(s + r - A)},$$

$$\left(\frac{dC_f}{dt}\right)^* = \Phi_l - (s + r - A)\frac{\Phi_i - \Phi_o - \Phi_{up}}{\alpha(s - A) - \beta(s + r - A)}. \tag{24}$$

Here SOM accumulation depends on microbial parameters and on the amount of mineral N that flows into and out of the soil (eqn 24). When there is a net mineral N input into soil ($\Phi_i - \Phi_o - \Phi_{up} > 0$), SOM accumulates leading to N sequestration. When mineral N is scarce ($\Phi_i - \Phi_o - \Phi_{up} = 0$), SOM accumulation and the underlying N sequestration cease. In this case, the SOM pool reaches equilibrium

(eqn 24). Note that in this case the FOM pool does not reach the equilibrium and increases continuously (unless $\Phi_l = 0$) owing to a lack of decomposition.

$N^* > 0$ requires $\Phi_i - \Phi_o - \Phi_{up} > 0$ (eqn 23). This is the condition in which the N-limited decomposers immobilize mineral N and survive. However, this is not realistic because net N supply to ecosystems is usually very small relative to the quantity of N required by vegetation ($\Phi_i - \Phi_o \ll \Phi_{up}$) (Vitousek & Howarth 1991). Consequently, the existence of a plant cover ($\Phi_{up} > 0$) leads to the exhaustion of soil mineral N and finally to the disappearance of the vegetation.

We conclude that the model cannot account for plant persistence, irrespective of the nutritional state considered for the decomposers (either C- or N-limited). When decomposers are limited by C, SOM accumulates despite the availability of N leading to a N deficit in the soil. When decomposers are limited by N, SOM accumulation depends on the availability of mineral N. However, by definition, N-limited decomposers immobilize mineral N only. This implies that plant N requirements must be met by net N inputs into a given ecosystem, which is not a realistic assumption. These results show that it is not possible to account for the empirical evidence of SOM accumulation and plant-decomposer coexistence by considering a single decomposer type.

Model 4

Using this model we test whether the inclusion of additional functional types of decomposers allows for plant-decomposer coexistence. Each of the two decomposer types can be either C- or N-limited. Thus, four scenarios must be considered for the analytical studies (Tables 2 and 3).

The two decomposer types are carbon-limited: case 1
Although two decomposer types are taken into account, the outcome in this case is qualitatively similar to that of the model with one decomposer type limited by C: whether the SOM pool decrease or increase depends on FOM-carbon flux and microbial parameters, and not on the availability of mineral N (Table 3). The simulated SOM accumulation induces a steady decrease in N availability owing to its sequestration in SOM. As the net N supply to ecosystems is usually low ($\Phi_i \approx \Phi_o$) the steady decrease in mineral N will finally lead to the exhaustion of soil mineral N.

The two decomposer types are nitrogen-limited: case 2
Again in this case the result is qualitatively the same as with one decomposer type limited by N: the change in SOM depends on microbial parameters and on the amount of mineral N that flows into and out of the soil, whereas the N mineral pool can reach a steady state (Table 3). However, the system persists if, and only if, the net N supply to the

Table 2 Non-trivial steady states for the four scenarios of model 4

Decomposer limitations	Equilibrium values
FOM decomposers limited by C SOM decomposers limited by C	$C_f^* = \dfrac{\Phi_l}{y + u}$ $C_{df}^* = \dfrac{u}{(y + u)(s + r)}\Phi_l$ $C_{ds}^* = \dfrac{y}{(s + r - A)(y + u)}\Phi_l$
FOM decomposers limited by N SOM decomposers limited by N	$C_{df}^* = \dfrac{iN*}{\alpha s - \beta(s + r)}$ $C_{ds}^* = \dfrac{iN*}{\alpha(s - A) - \beta(s + r - A)}$ $N* = \dfrac{\Phi_i - \Phi_o - \Phi_{up}}{2i}$
FOM decomposers limited by C SOM decomposers limited by N	$C_f^* = \dfrac{(s + r)}{u}C_{df}^*$ $C_{df}^* = \dfrac{(s + r - A)\left[\Phi_i - \Phi_o - \Phi_{up} + \beta\Phi_l + \alpha(A - s)\frac{\Phi_l}{s + r - A}\right]}{Ar\alpha}$ $C_{ds}^* = \dfrac{(s + r)\left[-(\Phi_i - \Phi_o - \Phi_{up} + \beta\Phi_l) + \alpha s\frac{\Phi_l}{s + r}\right]}{Ar\alpha}$ $N* = \dfrac{\alpha(s - A) - \beta(s + r - A)}{i}C_{ds}^*$
FOM decomposers limited by N SOM decomposers limited by C	$C_f^* = \dfrac{(s + r - A)}{y}C_{ds}^*$ $C_{df}^* = \dfrac{(s + r - A)\left[\Phi_i - \Phi_o - \Phi_{up} + \beta\Phi_l + \alpha(A - s)\frac{\Phi_l}{s + r - A}\right]}{Ar\alpha}$ $C_{ds}^* = \dfrac{(s + r)\left[-(\Phi_i - \Phi_o - \Phi_{up} + \beta\Phi_l) + \alpha s\frac{\Phi_l}{s + r}\right]}{Ar\alpha}$ $N* = \dfrac{\alpha s - \beta(s + r)}{i}C_{df}^*$

ecosystem brings more N than is absorbed by the plant cover ($\Phi_i - \Phi_o > \Phi_{up}$), which is unrealistic (Table 2).

The SOM decomposers are N-limited and the FOM decomposers are C-limited: case 3

As SOM decomposers are limited by N, an increase in N supply (a higher Φ_i for example) should increase SOM decomposer biomass. In the present case, an increase in N supply leads to a decrease in the biomass of SOM decomposers unless $s + r < 0$, which is not biologically possible. Thus, the combination of parameters resulting in this case should not arise in nature.

The SOM decomposers are C-limited and the FOM decomposers are N-limited: case 4

Once the plant persistence condition ($\beta\Phi_l - \Phi_{up} = 0$) is taken into account in eqn. (Tables 2 and 3) any change in

the SOM pool depends on the net N balance for the ecosystem alone. Net N input to the ecosystem ($\Phi_i - \Phi_o > 0$) increases the biomass of FOM decomposers that are N-limited (Table 2). As SOM decomposers are limited by energy, an increase in the biomass of FOM decomposers and in their uptake of FOM leads to a decrease in the biomass of SOM decomposers and, in turn, to a decrease in the rate of SOM mineralization. As a result of these changes, the SOM pool increases without reaching equilibrium (Table 3). When there is net N output from an ecosystem, the biomass of FOM decomposers decreases whereas the biomass of SOM decomposers increases, resulting in an increase in the rate of SOM mineralization. As a result, the SOM pool decreases. These results demonstrate the existence of a chain of interactions between the availability of N, the relative abundance of the two decomposer types, the SOM mineralization rate and finally

Table 3 Soil mineral N status and soil C dynamics for the four scenarios of the model 4 once the decomposers reach equilibrium

Decomposer limitations	Soil mineral N status at steady state of decomposers	Soil C dynamic at steady state of decomposers
FOM decomposers limited by C SOM decomposers limited by C	$\dfrac{dN}{dt} = \Phi_i - \Phi_o - \Phi_{up} + \beta\Phi_l - \alpha\dfrac{\Phi_l}{y+u}\left[\dfrac{y(s-A)}{s+r-A} + \dfrac{su}{s+r}\right]$	$\dfrac{dC_f}{dt} = \dfrac{\Phi_l}{y+u}\left[\dfrac{y(s-A)}{s+r-A} + \dfrac{su}{s+r}\right]$
FOM decomposers limited by N SOM decomposers limited by N	$N^* = \dfrac{\Phi_i - \Phi_o - \Phi_{up}}{2i}$	$\dfrac{dC_f}{dt} = (\Phi_i - \Phi_o - \Phi_{up})\left[\dfrac{A-s}{\alpha(s-A)-\beta(s+r-A)} + \dfrac{s}{\beta(s+r)}\right]$
FOM decomposers limited by C SOM decomposers limited by N	$N^* = \dfrac{\alpha(s-A)-\beta(s+r-A)}{i}C_{ds}^*$	$\dfrac{dC_f}{dt} = \dfrac{\Phi_i - \Phi_o - \Phi_{up} + \beta\Phi_l}{\alpha}$
FOM decomposers limited by N SOM decomposers limited by C	$N^* = \dfrac{\alpha s - \beta(s+r)}{i}C_{df}^*$	$\dfrac{dC_f}{dt} = \dfrac{\Phi_i - \Phi_o - \Phi_{up} + \beta\Phi_l}{\alpha}$

the change in the SOM pool. Such linkages allow for SOM accumulation to be regulated by the amount of N available in soil, which explains why the mineral N pool reaches an equilibrium (Table 3).

The system persists at steady state when it reaches equations (Table 2) with $\beta\Phi_l - \Phi_{up} = 0$ (plant persistence condition) and positive values for C_f^*, C_{df}^*, C_{ds}^*, N^*. $C_f^* > 0$ requires

$$s + r - A > 0. \tag{25}$$

Thus, the rate of SOM consumption by SOM decomposers must be lower than their turnover rate. As shown in model 1, this condition means that the long-term maintenance of SOM mineralization depends on the supply of FOM. $N^* > 0$ requires

$$\alpha s - \beta(s + r) > 0, \tag{26}$$

which indicates that the N : C ratio of FOM must be sufficiently lower in value than that of the decomposer biomass($\beta \ll \alpha$). If this condition is fulfilled, then the population growth of FOM decomposers depends on the availability of mineral N. Indeed, the N immobilization–mineralization flux

$$(\Phi_{IMf})^* = \alpha r C_{df}^* + (\beta - \alpha)(\Phi_f)^* = [\beta(s + r) - \alpha s]C_{df}^*$$

is negative in this case, which indicates that FOM decomposers immobilize N. Most incubations of plant litter and exudates induce net N immobilization (Recous *et al.* 1995; Mary *et al.* 1996), which suggests that FOM decomposers commonly depend on mineral N. This is supported by experiments showing the importance of gross N immobilization flux in soils (Hart *et al.* 1994; Mary *et al.* 1996). Thus, condition (26) seems realistic.

Taking into account the condition of plant persistence ($\beta\Phi_l - \Phi_{up} = 0$), $C_{df}^* > 0$ requires

$$\Phi_o - \Phi_i < \alpha(A - s)\frac{\Phi_l}{s + r - A}. \tag{27}$$

The term on the right refers to the N that flows out of the SOM pool and goes to the mineral pool (Fig. 3, $A > s$) when the equilibrium biomass of SOM decomposers reaches its maximal value ($\Phi_l/s + r - A$). At this equilibrium point, FOM decomposers are excluded by a lack of N and full FOM flux is absorbed by SOM decomposers. Thus, the system persists at steady state if the net N output from an ecosystem ($\Phi_o - \Phi_i$) remains lower than the mineral N production through SOM mineralization. As the mineral N production through SOM mineralization determined by isotopic dilution is commonly larger than the N balance for the ecosystem (Vitousek & Howarth 1991; Hart *et al.* 1994; Mary *et al.* 1996), condition (27) is likely to occur in soils. $C_{ds}^* > 0$ requires,

$$\Phi_i - \Phi_o < \alpha s \frac{\Phi_l}{s + r}. \tag{28}$$

The term on the right represents the N that flows out of the available pool and goes to the SOM pool (Fig. 3) when the equilibrium biomass of FOM decomposers reaches its maximal value ($\Phi_1/s + r$). Thus, the system persists at a steady state if the net N supply to the ecosystem ($\Phi_i - \Phi_o$) remains lower than the mineral N sequestration through SOM formation. As indicated above, the amount of N involved in the SOM mineralization-formation turnover is commonly larger than the N balance for the ecosystem (Vitousek & Howarth 1991; Hart *et al.* 1994; Mary *et al.* 1996). Thus, condition (28) is likely to occur in soils.

In this case, the model meets with conditions of feasibility (Daufresne & Loreau 2001) and stability (the Routh-Hurwith criteria for local stability, May 1974) (calculations not shown).

First, these results show that it is possible to account for the empirical evidence of the plant-decomposer coexistence by considering two major decomposer functional types, i.e. FOM decomposers and SOM decomposers, and their interactions with N. Second, they show that plants and decomposers are able to coexist when SOM decomposers are C-limited and FOM decomposers are N-limited (case 4). Third, they show that the mechanism of plant persistence is a chain of interactions between the availability of N, the relative abundance of the two decomposer types, the SOM mineralization rate and finally the change in SOM pool. When mineral N is abundant, SOM mineralization is low and the SOM pool increases. When mineral N becomes scarce, SOM mineralization accelerates and the SOM pool decreases. This acceleration of SOM mineralization releases mineral N that becomes available for plants. Finally, our results show that SOM accumulation depends on the N balance for the ecosystem until the net N input becomes saturating. In this latter case, FOM decomposers become C-limited and SOM accumulation is limited by FOM-carbon fluxes (results not shown).

DISCUSSION

Most SOM models assume that SOM decay only depends on the SOM pool and disregard the roles of the size and the diversity of microbial populations, that is, the presence of several microbial types and their interactions. However, experiments highlighting the importance of priming effects of organic matter indicate that the rate of SOM mineralization depends on the size of SOM decomposer populations and on the competition for energy and nutrient acquisition between several microbial functional types (Fontaine *et al.* 2003; Schimel & Weintraub 2003). Here, we show that models in which SOM decay is controlled by the size and the diversity of microbes populations result in qualitatively different predictions on C and N cycling and may explain some empirical results on SOM dynamics. Three novel predictions (presented below) emerge from our models.

Dependence of SOM decomposers (and mineralization) on FOM supply

Our four models of increasing complexity simulate the priming effect: the delivery of FOM to soil microbes increases the size of SOM decomposer population and, in turn, the rate of SOM mineralization. They also predict that the long-term maintenance of SOM decomposers relies on the supply of FOM. This indicates that without FOM supply, decomposers slowly disappear or become dormant and SOM mineralization ceases. Such a prediction explains how the lack of litter supply in deep soil horizons could lead to a lack of SOM mineralization. This reconciles the apparently contradictory results of SOM radiocarbon dating (associated with the traditional decomposition equation $dC/dt = -kC$), which suggest an extreme change in the decomposability of SOM along soil profiles, and those of direct measurements of the composition of SOM, which do not suggest such a change (Martel & Paul 1974; Rumpel *et al.* 2002). The C in deep soil horizons could also persist over long-time scales because this C is physically bound to soil minerals and exists in forms that decomposers cannot access (Torn *et al.* 1997). However, our prediction can be tested in the laboratory: if our assumption is right, then the supply of FOM to a soil sampled at depth should promote decomposer activity and mineralization of ancient soil C. Such an experiment should take care to preserve the physical structure of the soil.

Non-limited capacity of soils to accumulate SOM

Current models generally predict that the SOM pool of old soils have attained equilibrium. Such predictions result from the use of the traditional decomposition equation to depict SOM mineralization. If soil C mineralization depends on the soil C pool, then soil C mineralization increases with the increasing soil C content with time until the C output equals the C input indicating that SOM has attained equilibrium (Hénin & Dupuis 1945). However, when mineralization is modelled by an equation based on the size of decomposer populations, the mineralization of recalcitrant soil C does not increase with the soil C pool. In this case, the C pool does not necessarily reach equilibrium and may continuously increase (the prediction of models 2, 3 and 4). This prediction is consistent with the steady C accumulation in soils of many ecosystems for periods of even > 10 000 years (Syers *et al.* 1970; Schlesinger 1990).

Limitation of long-term SOM accumulation by available N

Another prediction of our theory is that the accumulation of SOM in soils depends on the availability of N. If one assumes that SOM accumulation and the underlying N

sequestration occurs irrespective of mineral N availability, then our model 3 shows that ecosystems are very likely to collapse owing to a N deficit for plants. It is obvious that plants and microbes coexist in most ecosystems. This coexistence is only possible if there is a feedback mechanism controlling the sequestration of nutrient. Our model 4 shows that such a mechanism could result from a chain of interactions between the availability of N, the relative abundance of populations of FOM and SOM decomposers, and finally the change in the SOM pool. When mineral N is abundant, the model predicts a low rate of SOM mineralization and an increasing SOM pool. When mineral N becomes scarce in the soil, the model predicts a relative increase in the populations of SOM decomposers, an acceleration of SOM mineralization and no accumulation of SOM. Such linkages are supported by recent experiments. Small increases in N availability change the microbial community structure (Waldrop *et al.* 2004), decrease the production of some enzymes involved in the degradation of complex organic matters (Carreiro *et al.* 2000), decrease the SOM mineralization rate (Hagedorn *et al.* 2003), and lead to an increase in soil C content (Fontaine *et al.* 2004b). We emphasize that limitation of SOM accumulation by N applies to N-limited ecosystems and does not concern fertilized agro systems.

Limitations of the models

Some of the assumptions of the model might seem unrealistic. A key assumption is that the input of FOM to the soil is continuous. Although this assumption seems reasonable in the case of natural soils where the plant cover is maintained over time, it does not hold true in the case of cultivated soils. In cultivated soils, the supply of FOM is discontinuous and soils can be maintained without vegetation over long periods during which soil N is mineralized and leached. Such dynamic aspects cannot be studied by an analysis at equilibrium. A second key assumption of our models is that the rate of SOM mineralization only depends on the size of decomposer populations. In fact, SOM availability could also limit SOM decay, at least in soils extremely poor in organic matter. Future models should take into consideration both the SOM pool size and the microbe population sizes, and their results should be compared with experimental data.

CONCLUSIONS

Despite its simplicity, our model 4 has potential implications for broader scale processes. Terrestrial ecosystems significantly buffer global warming by sequestering a quarter of anthropogenic emissions of CO_2 (0.8 Pg C year^{-1}) of which half results from the accumulation of refractory SOM

substances in soils (0.4 Pg C year^{-1}) (Schlesinger 1990; Houghton 2003). The future capacity of terrestrial ecosystems to act as a C sink depends on the soil sink potential and the factors controlling soil C accumulation. Our results combined with others (Syers *et al.* 1970; Schlesinger 1990) suggest that the soil sink is potentially unlimited and that the sequestration of refractory SOM may continue for millennia. However, the possible increase in C uptake by vegetation under elevated CO_2 should not increase the current SOM sequestration rate. Indeed, a decrease in soil mineral nutrients is expected as a consequence of a higher nutrient sequestration in SOM and a higher primary production (Díaz *et al.* 1993). Our model 4 predicts that such nutrient deficits will lead to an increase in SOM decomposer abundance and to a lack of SOM accumulation, which in turn maintains nutrient availability for plants. Finally, our model predicts that C storage in terrestrial ecosystems depends on the ability of ecosystems to sequester more nutrients.

We progressively made our model more complex in order to find the minimal set of mechanisms required to account for major ecosystem functions. The results suggest that it is not possible to account for plant-decomposer coexistence considering only one decomposer functional type. As this coexistence is the key to primary production, the presence of several microbial types and their interactions (Fontaine *et al.* 2003, 2004b) seems to be a pre-requisite for ecosystem persistence.

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