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A theoretical analysis of nonlinearities and feedbacks in soil carbon and nitrogen cycles

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Abstract

Analytical formulations of soil carbon and nitrogen cycles are used to explore the effects of model nonlinearities and feedbacks on the resulting dynamics. Two particular aspects are addressed: (i) nonlinearities in the decomposition rate of soil organic matter and (ii) nitrogen limitation feedbacks on microbial activity and plant–microbe competition. Although linear models of decomposition are more typical in the literature, nonlinear models accounting for the coupling between microbial biomass and its substrate have also been proposed. In deterministic conditions, linear models behave like exponential decay functions, while nonlinear models may also show fluctuating behavior, with dynamic bifurcations between stable-node and stable-focus equilibria as a function of the climatic parameters (e.g., soil moisture and temperature). Both data-model comparison and linear stability analysis support the conclusion that linear models are less suited to describe the soil fluctuating dynamics that arise under certain conditions. A second strong nonlinearity appears when the nitrogen-limitation feedback on decomposition is analyzed. Nitrogen limitation is often established when the substrate of the microbes is N-poor, and/or the competition with plants for mineral N is strong. Such conditions mainly occur when a large fraction of the microbial community cannot meet its nitrogen demand through organic N assimilation, so that mineral N is used. On the contrary, when the microbial community predominantly assimilates organic nitrogen, the occurrence of nitrogen-limitation is less likely and mineralization is given by microbial N surplus. The first case is traditionally modeled by the mineralization–immobilization turnover (MIT) scheme, while the second by the direct assimilation (DIR) scheme. However, since organic N assimilation and mineral N immobilization likely occur simultaneously because of soil heterogeneity and coexistence of different microbial communities, the two schemes only represent extreme cases. Thus, we combine them in a flexible model framework (parallel scheme) and explore how different efficiencies of organic nitrogen assimilation, mineral nitrogen availability and climatic factors control the outcome of plant–microbe competition. We conclude that models accounting only for the DIR pathway implicitly assume that microbes are superior competitors over plants, while models implementing only the MIT pathway might be too sensitive to N-limitation.

Keywords: Mineralization; Immobilization; Mineralization–immobilization turnover; Direct hypothesis; Microbial biomass; Nonlinear dynamics; SOM model; Soil moisture; Plant–microbe competition; Water stress

1. Introduction

Carbon and nitrogen cycles in soils are driven by both environmental forcing and biologic activity. At the same time, they are also constrained by the chemical composition of soil organic matter (SOM) and by the nutrient demand of microbes and plants. Biotic and abiotic components interact nonlinearly with the processes of SOM decomposition and mineralization, giving rise to a number of complex relationships and feedbacks (Smith et al., 1998). Such feedbacks have been theoretically analyzed by means of mathematical models, which have been tested against experimental datasets (Powlson et al., 1996; Smith et al., 1997) and compared in terms of prediction consistency (VEMAP members, 1995) as well as model resolution and complexity (de Willigen, 1991; Paustian, 1994; McGill, 1996; Molina and Smith, 1998; Smith et al., 1998; Benbi and Richter, 2002). However, only few sporadic attempts (e.g., Wu and McGechan, 1998) have been made to compare the

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underlying structures and analytical formulations, and to understand their effects on the simulated dynamic behavior of soil biogeochemical cycles.

To address this aspect, we focus on two major issues in biogeochemical modeling: (i) the coupling between microbial biomass dynamics and decomposition process and (ii) the different pathways of nitrogen mineralization and immobilization, and their effects on N limitation.

The first issue is of particular interest, as most biogeochemical models assume first-order decay rates for SOM and thus do not explicitly include the role of microbial biomass in the decomposition process. However, decomposition is clearly driven by microbial activity (Schimel and Weintraub, 2003; Fang et al., 2005; Neill and Gignoux, 2006), which in turn is particularly sensitive to environmental fluctuations and long-term climatic changes (Smith et al., 1998). To account for this coupling, nonlinear models depending on both substrate availability and microbial biomass concentrations have been proposed. In contrast to the linear donor-controlled models, the nonlinear approaches resemble the Lotka–Volterra type of equations (e.g., Murray, 2002), where both donor (i.e., SOM carbon) and consumer (microbial biomass) are involved in the process. Analogous equations have been used in population ecology to describe dynamical oscillations in the predator–prey dynamics. Indeed, since microbial biomass may be regarded as a predator of organic substrates, dynamical oscillations are not unsurprising and have actually been reported in both modeling simulations (Bosatta and Berendse, 1984; D'Odorico et al., 2003; Manzoni et al., 2004) and short-term experimental studies (Semenov et al., 1999; Zelenev et al., 2005b). Considering that commonly employed linear models of soil biogeochemistry only display pure decay functions (Bolker et al., 1998; Baisden and Amundson, 2003), it is clear that alternative nonlinear formulations should be used to model such complex dynamics.

Our second issue, which regards the mineralization–immobilization pathways and N limitation, involves the whole soil nitrogen cycle and in particular the relationship between plants and microbes. While on the one hand plants and microbes are in competition for soil nutrients, N in particular, on the other hand their interaction is mutualistic, since plant residues constitute the main substrate for microbial biomass that in turn produces inorganic nitrogen used by plants (Harte and Kinzig, 1993; Brady and Weil, 1996). The competitive interaction is regulated by the relative distribution of roots and microbes in the soil (e.g., Schimel et al., 1989; Zak et al., 1990; Kaye and Hart, 1997), but it also depends on the pathway followed by the mineralized N. Two different schemes have been developed to model these complex pathways at the macroscopic scale, the mineralization–immobilization turnover (MIT) scheme (Jansson, 1958), and the direct assimilation scheme (hereafter referred to as DIR; Molina et al., 1983). The MIT scheme maintains that all organic nitrogen is mineralized to ammonium prior to assimilation by soil microbial biomass. In this way, the pool of mineral N can be exploited by both microbes and plants. On the contrary, the DIR scheme assumes that the exocellular enzymes hydrolyze the organic compounds to their basic amino acids, which are directly assimilated by the microbes, thus allowing them to retain the needed N, and only release the surplus (Barak et al., 1990; Drury et al., 1991; Barraclough, 1997). Although the MIT scheme seems to better describe the mineralization process at the macroscopic scale in certain soils (Hadas et al., 1992a), the DIR scheme is physiologically more realistic, since it accounts for microbial assimilation of low molecular weight amino acids (Barak et al., 1990; Vinolas et al., 2001). It should be noted, however, that in heterogeneous soils mineralization of organic N and immobilization of mineral N often occur simultaneously (Hadas et al., 1992b; Saetre and Stark, 2005). Mineralization predominantly occurs in N-rich micro-sites, while in N-poor micro-sites both mineral and organic sources of N are used, depending on their relative availability (Schimel and Bennett, 2004). The DIR scheme may thus be more suited to describe soils with both N-rich and N-poor micro-sites actively mineralizing N, while the MIT scheme may better model soils with N-poor micro-sites predominantly immobilizing the available mineral N. Thus, at the macroscopic level a combination of the DIR and MIT pathways is typically observed (Hadas et al., 1992b; Garnier et al., 2003). We will refer to this as the parallel hypothesis (PAR, Barraclough, 1997). So far, however, these alternative hypotheses have not been thoroughly compared to assess how they affect the simulated N cycle and the outcome of plant–microbe competition.

In this paper, we hypothesize that the nonlinearity of the decomposition function and the choice of the mineralization pathway significantly alter the model ability to resolve some specific SOM–microbe–plant interactions. More specifically, our objectives are:

(i) to analyze the dynamical effects of linear and nonlinear decomposition formulations, under different climatic conditions;
(ii) to investigate the role played by the N mineralization pathway and climatic factors in microbial N limitation and plant–microbe competition for mineral N.

The effects of nonlinearities in decomposition are studied by means of a simplified soil C model, which is then extended to include N dynamics. In agreement with the PAR hypothesis, the DIR and MIT pathways are merged into a flexible model framework, providing a continuum to connect these two antithetic N assimilation schemes.

2. Methods

2.1. Soil C dynamics: microbial control of decomposition processes

In this section, we examine the interactions of microbial biomass and soil substrate in the decomposition process,

interpreted as a donor–consumer relationship. The analytical formulations of different decomposition models are discussed with emphasis on their linear or nonlinear character. Comparisons with experimental results and effects of climatic parameters on the dynamic behavior of the models are described in Section 3.1.

2.1.1. General models of SOM decomposition

Consider a simplified soil system where a single compartment of carbon substrate (C_S) interacts with the microbial biomass (C_B) (Fig. 1). The SOM carbon fraction (SOM-C) is assumed to be a passive substrate, while the microbial pool includes all the biotic components of the soil system. The variables are expressed in terms of mass of carbon per unit volume of soil (e.g., $gC\,m^{-3}$); the system is assumed to be open, with a plant residue input (ADD) and an output of mineralized carbon to the atmosphere. The nitrogen fluxes are neglected, since for now the focus is on the relationships between substrate and decomposers in the absence of any nutrient limitation. The carbon balances for the substrate and the microbe pools can thus be expressed as

$$\frac{dC_S(t)}{dt} = ADD - DEC' + BD, \tag{1}$$

$$\frac{dC_B(t)}{dt} = (1-r)DEC' - BD, \tag{2}$$

where DEC' is the flux of decomposed carbon when nutrients are not limiting. A factor accounting for possible nitrogen limitation, φ, will be introduced in Section 2.2, and the decomposition will be consequently modified (i.e., $DEC = \varphi DEC'$). The heterotrophic respiration is $rDEC'$, and $1-r$ is the carbon utilization efficiency (assimilated over decomposed carbon). For simplicity, microbial decay, BD, is modeled as first-order kinetics, $BD = k_B C_B$, as in most biogeochemical models (e.g., Parton et al., 1987). Nonlinear decay functions, where BD is assumed to be an inverse function of the available substrate, have also been used (e.g., Blagodatsky and Richter, 1998; Zelenev et al., 2000).

The definition of the decomposition function is more complex, and different formulations have been used (see the reviews by de Willigen, 1991; Paustian, 1994; McGill, 1996; Whitmore, 1996b; Molina and Smith, 1998; Wu and McGechan, 1998). Most of the models use simple first-order kinetics with respect to the substrate concentration in the source pool (hereafter referred to as linear model),

$$DEC' = k_S C_S(t), \tag{3}$$

where k_S is the first-order rate constant, in general a function of the chemical composition of the SOM compounds and environmental conditions, mainly soil moisture and soil temperature (see Section 2.1.2). The assumption behind this formulation is that soil organisms respond so quickly to changes in substrate availability, that their abundance never limits the decomposition rate (Paustian, 1994; Hansen et al., 1995; Smith et al., 1998). For this reason, decomposition is treated as a donor-controlled process, where the decomposers are assumed to be a static sink of substrate.

Recently, this linear approach has been challenged on the ground that SOM chemical breakdown is not only dependent on the amount of decomposable material, C_S, but it also relies on the activity of biologically released enzymes (Schimel and Weintraub, 2003, Fang et al., 2005; Neill and Gignoux, 2006). This tight coupling between substrate and biological processes is necessary, in particular, while modeling short-term C and N dynamics (Blagodatsky and Richter, 1998; Zelenev et al., 2000), but it might be relevant also in medium- (Whitmore, 1996a) and long-term analyses (Smith et al., 1998). Accordingly, Eq. (3) may be substituted by a nonlinear Michaelis–Menten rate equation (Murray, 2002), where the role of exoenzymes is explicitly accounted for. Assuming that the enzyme concentration is proportional to the microbial biomass, one obtains (Panikov and Sizova, 1996; Blagodatsky and Richter, 1998)

$$DEC' = k_S C_B(t)\frac{C_S(t)}{K_m + C_S(t)}, \tag{4}$$

where K_m is the Michaelis constant. Some models even include microbial density negative feedbacks on decomposition (Garnier et al., 2001), or more complex nonlinear expressions, including both microbial density and co-metabolism effects (McGill et al., 1981). The drawback of such detailed formulations, however, is a heavier model parameterization. Thus, in many cases, since substrate concentrations in natural soils are generally low, a reasonable compromise between Eqs. (3) and (4) can be found as

$$DEC' = k_S C_S(t) C_B(t), \tag{5}$$

obtaining a multiplicative expression which still includes the basic coupling of decomposers and substrate (Harte and Kinzig, 1993; Whitmore, 1996a; Schimel and Weintraub, 2003; Porporato et al., 2003).

2.1.2. Soil moisture and soil temperature effects on microbial activity

The decomposition rate k_S is generally modeled assuming a multiplicative effect of soil moisture and temperature

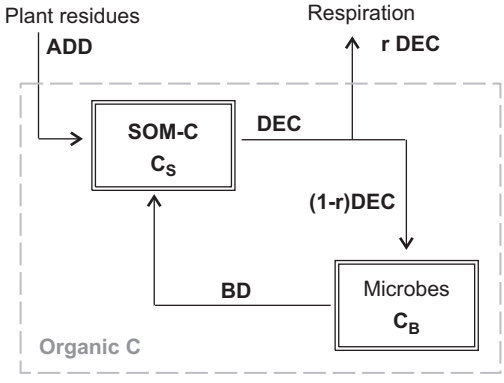

Fig. 1. Simplified scheme of the carbon model described by Eqs. (1) and (2).

(Rodrigo et al., 1997),

$$k_S = k_S^* f_s(s) f_T(T), \tag{6}$$

where k_S^* is the potential decomposition rate, while $f_s(s)$ and $f_T(T)$ are reduction factors accounting for soil moisture (s, in terms of fraction of water filled pore space) and soil temperature (T), respectively. The temperature effect can be simply modeled as a quadratic function of T, normalized in order to have $0 \leqslant f_T(T) \leqslant 1$ (Ratkowsky et al., 1982; Katterer and Andrén, 2001).

Microbial activity depends on s in a strongly nonlinear way, since at low soil moisture water is a limiting factor (Stark and Firestone, 1995), resulting in limited substrate diffusivity and low cellular water potential, while oxygen limitation occurs near saturation conditions (Skopp et al., 1990; Zak et al., 1999; Schjonning et al., 2003). Hence, following Gusman and Marino (1999) and Porporato et al. (2003), the corrective coefficient f_s(s) may be modeled as (Fig. 2)

$$f_s(s) = \begin{cases} 0 & s \leqslant s_B, \\ \dfrac{s - s_B}{s_{fc} - s_B} & s_B < s \leqslant s_{fc}, \\ \dfrac{s_{fc}}{s} & s_{fc} < s \leqslant 1, \end{cases} \tag{7}$$

where s_{fc} is the soil field capacity and s_B the microbial biomass stress point (Table 1), below which (in analogy with the plant wilting point) biological activity is completely halted. The value of s_B depends on the physiological adaptation of the single microbial groups or species to reduced water potential (Griffin, 1980), and allows us to account for different adaptation strategies to water stress.

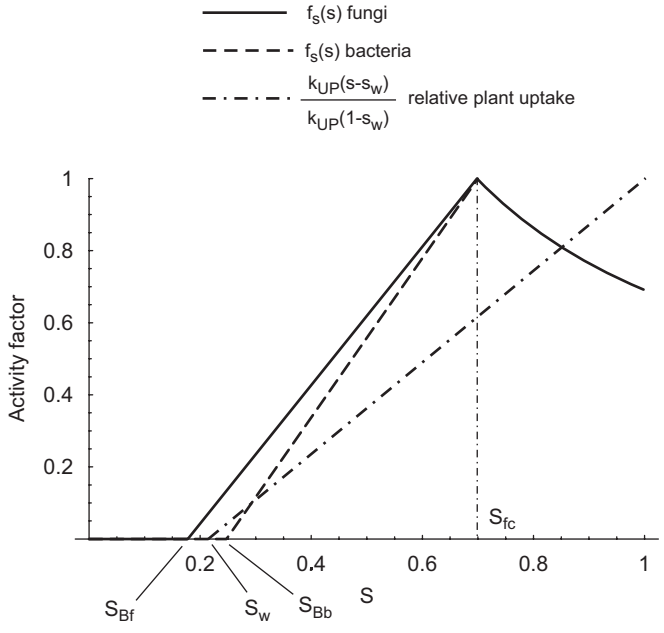

Fig. 2. Normalized rates of bacterial and fungal activity (Eq. (7)) and plant N uptake (Eq. (15)) as a function of soil moisture s (parameter values are reported in Table 1).

For example (Fig. 2), certain fungi are adapted to survive at water potentials as low as −8 MPa, while more sensitive bacteria often cease their activity at around −2 MPa, which may even be above the plant wilting point (Freckman, 1986; Schwinning and Sala, 2004).

2.2. Coupled C–N dynamics: mineralization–immobilization pathways and N-limitation feedbacks

Different conceptual models of nitrogen transformation pathways are critically reviewed in this section and included in a single general model, which is then analyzed in deterministic conditions in Section 3.2.

2.2.1. Modeling N cycle and coupled C and N dynamics

The simplified C cycle sketched in Fig. 1 is complemented by the N flow scheme shown in Fig. 3, which is the basis for this analysis of N dynamics. Plant residues are assumed to be the only N input, while plant mineral nitrogen uptake is the only output of the system; for simplicity, other inputs and outputs, such as atmospheric deposition, denitrification, and leaching, are neglected. Mass balances for the SOM-N (N_S) and microbial biomass nitrogen (N_B) compartments are directly derived from the corresponding C balances, through the C/N ratios of the different pools (e.g., Parton et al., 1987; Hansen et al., 1991; Katterer and Andrén, 2001; Porporato et al., 2003), while the balance equation of mineral nitrogen (N) depends on gross mineralization and immobilization, as well as on plant uptake. With these assumptions, the C–N model can be written as

$$\frac{dC_S(t)}{dt} = \mathrm{ADD} - \mathrm{DEC} + \mathrm{BD}, \tag{8}$$

$$\frac{dN_S(t)}{dt} = \frac{\mathrm{ADD}}{(C/N)_{\mathrm{ADD}}} - \frac{\mathrm{DEC}}{(C/N)_S} + \frac{\mathrm{BD}}{(C/N)_B}, \tag{9}$$

$$\frac{dC_B(t)}{dt} = (1 - r)\mathrm{DEC} - \mathrm{BD}, \tag{10}$$

$$\frac{dN_B(t)}{dt} = \eta \frac{\mathrm{DEC}}{(C/N)_S} - \Phi - \frac{\mathrm{BD}}{(C/N)_B}, \tag{11}$$

$$\frac{dN(t)}{dt} = (1 - \eta)\frac{\mathrm{DEC}}{(C/N)_S} + \Phi - \mathrm{UP}. \tag{12}$$

DEC is modeled according to Eq. (5), and multiplied by a variable $\varphi[(C/N)_S, N]$, accounting for the inhibiting effect of low nitrogen availability on microbial processes (Recous et al., 1995; Mary et al., 1996; see Section 2.2.2),

$$\mathrm{DEC} = \varphi[(C/N)_S, N]\mathrm{DEC}'. \tag{13}$$

The variable φ modifies the decomposition rate by acting on the microbial activity and allowing to switch from substrate- (i.e., controlled by C_S) to nitrogen-limited (i.e., controlled by N) growth. Note that when DEC is nonlinear (Eqs. (4) and (5)), such nonlinearity is propagated to the N cycle as well, in agreement with experimental evidence of a

Table 1
Parameters characteristic of a temperate forest ecosystem and used in the simulations, unless otherwise specified

Parameter	Symbol	Value	Units	Reference
Plant wilting point[a]	s_w	0.22 (−3)	– (MPa)	Laio et al. (2001)
Fungi stress point[b]	s_{Bf}	0.18 (−8)	– (MPa)	Freckman (1986)
Bacteria stress point[a]	s_{Bb}	0.24 (−2)	– (MPa)	Freckman (1986)
Soil field capacity[a]	s_{fc}	0.7 (−0.01)	– (MPa)	Schjonning et al. (2003)
Annul C input in the soil	ADD	3.2	$g\,m^{-3}\,d^{-1}$	Finzi et al. (2002)
Microbial composition	$(C/N)_B$	8	$g\,C\,(g\,N)^{-1}$	McGill et al. (1981)
Composition of added litter	$(C/N)_{ADD}$	82	$g\,C\,(g\,N)^{-1}$	Finzi et al. (2002)
Respired C fraction	r	0.6	—	McGill et al. (1981)
Microbial decay rate	k_B	7×10^{-3}	d^{-1}	Bosatta and Agren (1994)
SOM decomposition rate[b]	k_S*	1.8×10^{-5}	$m^3\,d^{-1}(g\,C_B)^{-1}$	Chosen value
Max. immobilization rate	k_I*	10^{-3}	$m^3\,d^{-1}(g\,C_B)^{-1}$	Chosen value
Plant uptake rate	k_{UP}	0.1	d^{-1}	Chosen value

[a]Relative soil moisture is computed from water potentials (in parenthesis) through the water retention curve of a loamy soil (parameters after Hacke et al., 2000; Laio et al., 2001). Soil moisture is non dimensional; water potentials are expressed in MPa.
[b]Value and units relative to the multiplicative decomposition model (Eq. (5)).

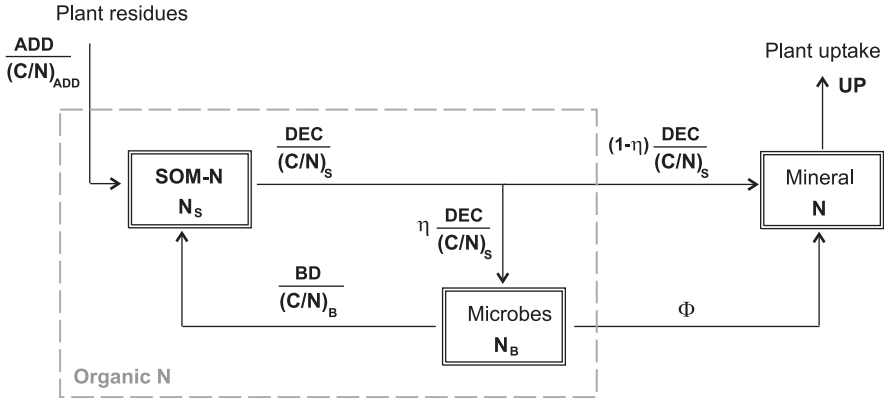

Fig. 3. Simplified scheme of the carbon and nitrogen model described by Eqs. (8)–(12).

correlation between mineralization and microbial activity and respiration (Hart et al., 1994; Mary et al., 1998; Luxøi et al., 2006). The partition coefficient η, first introduced by Garnier et al. (2001), and hereafter referred to as "organic N assimilation efficiency" defines which fraction of the decomposed organic N enters directly the microbial biomass following the DIR scheme, while the fraction $1-\eta$ is mineralized through the MIT pathway. When $\eta = 1$, the model describes the DIR scheme and the equations for mineralization are the same as in, e.g., Molina et al. (1983) and Parton et al. (1987). On the contrary, when $\eta = 0$, all the nitrogen bounded to the decomposed material is transferred to the mineral nitrogen pool according to the MIT hypothesis, as in Van Veen et al. (1985) and Hadas et al. (1987). Hence, this general model bridges the two previously proposed schemes, in agreement with the PAR hypothesis.

Assuming that the C/N ratio of the microbial biomass, $(C/N)_B$, remains constant, the mass balance equation for N_B becomes redundant once the equation for C_B is given. The assumption of constant $(C/N)_B$ has two major implications: (i) microbes have to assimilate carbon and nitrogen in fixed proportions; (ii) the less available element between C and N limits their growth rate. The amount of carbon assimilated during decomposition is $(1-r)$DEC, but the N assimilated is $\eta \mathrm{DEC}(C/N)_S^{-1}$ (Fig. 3). Since in general these two fluxes do not provide the correct proportion of C and N to the microbes, a nitrogen imbalance is created and the term Φ in Eqs. (11) and (12) accounts for that (e.g., Molina et al., 1983; Hansen et al., 1991; Katterer and Andrén, 2001; Porporato et al., 2003). When the N content of SOM is low (i.e., $(C/N)_S$ is high), microbes generally need to immobilize nitrogen ($\Phi<0$), while they have a N surplus when SOM nitrogen content is high ($\Phi>0$). From Eqs. (10) and (11), and imposing constant $(C/N)_B$, it can be shown that

$$\Phi = \mathrm{DEC}\left[\frac{\eta}{(C/N)_S} - \frac{1-r}{(C/N)_B}\right]. \tag{14}$$

The last term of the mineral nitrogen balance equation (Eq. (12)) is plant uptake, UP, which mainly depends on the available inorganic nitrogen and its mobility in the soil. For simplicity, we neglect any distinction between the diffusive (active) and the transpiration-driven (passive)

nitrogen fluxes to the roots and model plant uptake through a first order kinetic with respect to N (e.g., Clarke and Barley, 1968), with the rate coefficient linearly dependent on soil moisture above plant wilting point (s_w),

$$\mathrm{UP} = \begin{cases} 0 & s \leqslant s_w, \\ k_{\mathrm{UP}}(s - s_w)N & s_w < s \leqslant 1. \end{cases} \tag{15}$$

Fig. 2 compares the rate of plant nitrogen uptake and microbial activity, $f_s(s)$ (Eq. (7)) when the fungal stress point, s_{Bf}, is lower than plant wilting point, s_w, which in turn is assumed to be lower than the bacterial stress point, s_{Bb} (e.g., Freckman, 1986; see also Table 1).

2.2.2. Gross N mineralization and immobilization, and N-limitation modeling

Since Φ (Eq. (14)) only quantifies the N imbalance of the microbial community, it is necessary to define net and gross mineralization and immobilization, which on the contrary are more physically meaningful and that, to a certain extent, can be measured. The net flux of nitrogen exchanged between the inorganic N pool and the organic N compartment (Eq. (12)) is given by the sum of the N fluxes associated with decomposition, but not directly assimilated by microbes, $(1-\eta)\mathrm{DEC}(C/N)_S^{-1}$, and the term Φ (Fig. 3). When the sum of these two terms is positive, it represents the N net mineralization ($\mathrm{MIN_{net}}$), otherwise it is the net immobilization ($\mathrm{IMM_{net}}$),

$$\mathrm{MIN_{net}} = \max\left\{(1-\eta)\frac{\mathrm{DEC}}{(C/N)_S} + \Phi, 0\right\}, \tag{16}$$

$$\mathrm{IMM_{net}} = -\min\left\{(1-\eta)\frac{\mathrm{DEC}}{(C/N)_S} + \Phi, 0\right\}. \tag{17}$$

In Eqs. (16) and (17), both fluxes are defined as positive quantities. When N transformations are modeled using only net fluxes, it is implicitly assumed that the corresponding gross fluxes are similarly controlled by environmental and biological factors. This is not the case for gross mineralization and immobilization, since major differences in the controlling factors arise under C- or N-limited conditions. Following Eqs. (16) and (17), N gross mineralization and immobilization can be obtained as

$$\mathrm{MIN_{gross}} = (1-\eta)\frac{\mathrm{DEC}}{(C/N)_S} + \max\{\Phi, 0\}, \tag{18}$$

$$\mathrm{IMM_{gross}} = -\min\{\Phi, 0\}. \tag{19}$$

The organic N assimilation efficiency η exerts a major control on both $\mathrm{MIN_{gross}}$ and $\mathrm{IMM_{gross}}$. In fact, when $\eta = 1$ (DIR), net and gross fluxes coincide, and the N recycling between microbes and mineral N is minimized. On the contrary, when $\eta = 0$ (MIT), all decomposed N is first mineralized and then immobilized, thus maximizing its recycling. Hence, decreasing η enhances gross mineralization and results in N accumulation in the mineral pool, where it becomes available to plants and object of competition between plants and microbes.

Assuming that φ controls decomposition and immobilization in a similar way and following Eqs. (13) and (14), one may express $\mathrm{IMM_{gross}}$ as

$$\mathrm{IMM_{gross}} = \varphi[(C/N)_S, N]\mathrm{IMM_{pot}}, \tag{20}$$

where the potential immobilization rate, $\mathrm{IMM_{pot}}$, is stoichiometrically defined as the positive N flux needed by the microbes to grow at a C-limited rate $(1-r)\mathrm{DEC}'$,

$$\mathrm{IMM_{pot}} = \max\left\{\mathrm{DEC}'\left[\frac{1-r}{(C/N)_B} - \frac{\eta}{(C/N)_S}\right], 0\right\}. \tag{21}$$

Under C-limiting conditions, $\mathrm{IMM_{pot}}$ in Eq. (21) coincides with gross immobilization (Eq. (19)) and with the definition of Φ in Eq. (14), because $\varphi = 1$ and inorganic nitrogen availability is sufficient to meet the microbial N demand. When the N content of the substrate is low (i.e., high $(C/N)_S$), $\mathrm{IMM_{pot}}$ may overcome the rate at which mineral N is made available. In this case, the availability of mineral N becomes the more limiting factor for microbial growth. Following Porporato et al. (2003), we model the onset of N limitation introducing a maximum rate of gross immobilization, $\mathrm{IMM_{max}}$,

$$\mathrm{IMM_{max}} = k_I C_B N, \tag{22}$$

where the immobilization rate constant, k_I, in general depends on soil moisture and soil temperature, in analogy with k_S (Eq. (6)). Thus, gross immobilization is assumed to be unrestricted, provided that $\mathrm{IMM_{pot}} \leqslant \mathrm{IMM_{max}}$, while, otherwise, φ must become lower than one to ensure $\mathrm{IMM_{gross}} = \mathrm{IMM_{max}}$ (Porporato et al., 2003),

$$\varphi = \frac{\mathrm{IMM_{max}}}{\mathrm{IMM_{pot}}} = \frac{k_I N}{k_S C_S[(1-r)/(C/N)_B - \eta/(C/N)_S]}. \tag{23}$$

Hence, the function φ provides a switch mechanism from C-limited decomposition and demand-controlled immobilization, when $\varphi = 1$, and N-limited decomposition and immobilization, when it is lower than one. Also, this formulation bridges the two approaches which assume that either $\mathrm{IMM_{pot}}$ (Bosatta and Berendse, 1984; Schimel and Weintraub, 2003) or φ (Parnas, 1975; McGill et al., 1981; Harte and Kinzig, 1993) controls gross immobilization.

3. Results and discussion

3.1. Climatic controls and nonlinearities of C dynamics

To assess the effects of the different formulations of decomposition described by Eqs. (3) (linear model), (4) (Michaelis–Menten model), and (5) (multiplicative model), we first compare their ability to describe fluctuating dynamics of microbial biomass (Fig. 4). Second, we study Eqs. (1) and (2) as a dynamical system in the idealized case of constant soil moisture, temperature, and plant residue input in the SOM pool, and assess how the climatic factors control their dynamic behavior.

Linear and nonlinear decomposition models have been extensively validated against experimental datasets (e.g.,

Andrén and Paustian, 1987; Whitmore, 1996a), but never in conditions leading to fluctuating dynamics of SOM or microbial biomass not due to external forcing. Fluctuations induced by microbial biomass and substrate interactions were reported in rhizosphere experiments (Semenov et al., 1999; Zelenev et al., 2005b) and was simulated by an ad hoc model based on Michaelis–Menten decomposition kinetics (Eq. (4)) and a nonlinear function of microbial decay (Zelenev et al., 2000). The performance of this specifically designed model is compared in Fig. 4 with the simpler multiplicative and linear models of Eqs. (3) and (5). The nonlinear decay function used by Zelenev et al. (2000) introduces a further feedback between biological activity and its substrate, resulting in enhanced oscillation amplitudes (Fig. 4) and good fit of the measured oscillations (correlation coefficient $R = 0.66$). The multiplicative model (Eq. (5)), although maintaining its original linear expression for microbial decay, is able to simulate the oscillatory behavior, but the resulting trajectories appear to be over-damped ($R = 0.43$). On the contrary, the linear model (Eq. (3)) only captures the general trend of microbial biomass, but it cannot describe its fluctuations ($R = 0.23$). Thus, nonlinearity seems to be necessary to explain these oscillations. Moreover, although employing the same number of parameters, the multiplicative model appears more flexible than the linear one, and may represent a useful compromise between the linear model and more complex nonlinear formulations.

It is also interesting to explore the role of parameter values on model dynamic behavior around equilibrium. Stability analysis by Bolker et al. (1998), Baisden and Amundson (2003) and Manzoni et al. (2004) suggest that the qualitative behavior around equilibrium conditions is more sensitive to the type of coupling among the variables than to the number of pools and their connections. Hence, we can study Eqs. (1) and (2) instead of more complex multi-compartment models and expect a qualitatively similar behavior. We refer to Argyris et al. (1994) for details about linear stability analysis and only recall here that real negative eigenvalues imply exponential convergence to a stable equilibrium, while complex conjugate values indicate convergence through damped oscillations. Purely imaginary eigenvalues, leading to limit cycles are not likely to occur here, for the soil carbon cycle is intrinsically open and strongly dissipative, e.g., the respired fraction of decomposition is in the range 0.4–0.8 (McGill et al., 1981). Clearly, the equilibrium values and their eigenvalues (Table 2) depend on both model type and parameter values. The sensitivity to variations of the kinetic rate constant k_S is of particular importance, since it generally includes the dependence of decomposition on climatic forcing (Section 2.1.2) and, possibly, nitrogen limitation. The linear model (Eq. (3)) does not change its qualitative dynamic behavior around the equilibrium, and the steady state is always a stable node, since both eigenvalues are real and negative. However, the actual value of the equilibrium point as well as the initial transient depend on k_S (Table 2). Similar results were found by Bolker et al. (1998) and Baisden and Amundson (2003), who showed that their multi-compartment biogeochemical models actually behave like pure decay functions.

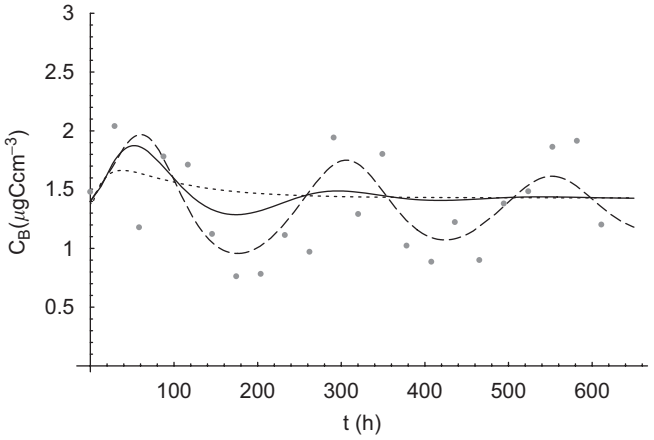

Fig. 4. Comparison of different model simulations with measured microbial biomass concentrations. All models share the same initial conditions, external input (ADD) and number of state variables (i.e., C_B and C_S, as in Eqs. (1) and (2)). Only the decomposition and microbial decay functions have been changed; the kinetic constants of the multiplicative and linear models have been estimated reducing the equations in Zelenev et al. (2000) to the simpler expressions in Eqs. (3) and (5). Original space-dependent data have been transformed in time-dependent following Zelenev et al. (2000, 2005a). •, Data (Semenov et al., 1999); ——, BACWAVE (Zelenev et al., 2000); —, Multiplicative model (Eq. (5)); - - - - -, Linear model (Eq. (3)).

When either Eq. (4) or (5) is used for decomposition modeling, a richer dynamic behavior is observed, because changes in the rate constant, k_S, may dramatically affect the eigenvalues and result in bifurcations. Fig. 5 shows how the values of the eigenvalues depend on k_S in the multiplicative model of Eq. (5). When the rate constant is low, as for example in arid and semiarid environments (see Fig. 2), the eigenvalues are complex conjugates, and the equilibrium point is a stable focus, reached through damped oscillations. When k_S is high, the imaginary parts disappear and the dynamics converge to a stable node. However, due to the nonlinear character of Eq. (7), moving from low soil moisture to values close to saturation, while keeping temperature constant (dot–dashed line in Fig. 6a), two dynamic bifurcations occur. For soil moisture below the microbe stress point ($s < s_B$), biological activity is not sustained and the equilibrium is characterized by zero biomass. When soil moisture is increased above s_B, microbial activity is low, but sufficient to sustain decomposition, resulting in a stable focus with damped oscillations to equilibrium. Approaching field capacity, the first bifurcation takes place and, in the region where the decomposition is more efficient, the equilibrium point becomes a stable node. The situation is inverted at high soil moisture values, where damped oscillations leading to a stable focus reappear.

Table 2
Substrate and microbial biomass at steady state (C_B* and C_S*, respectively) and eigenvalues ($\lambda_{1,2}$) of the system of Eqs. (1) and (2) for different decomposition models, with $\alpha = 2rk_B$ and $\beta = k_S(1-r)$

Model	Linear	Multiplicative	Michaelis–Menten
DEC	$k_S C_S$	$k_S C_S C_B$	$k_S C_B C_S/(K_m + C_S)$
Eq.	(3)	(5)	(4)
C_B*	$2\mathrm{ADD}(1-r)/\alpha$	$2\mathrm{ADD}(1-r)/\alpha$	$2\mathrm{ADD}(1-r)/\alpha$
C_S*	$\mathrm{ADD}/k_S r$	k_B/β	$\frac{k_B K_m}{\beta - k_B}, \beta > k_B$
$\lambda_{1,2}$	$-\frac{k_S + k_B}{2}\left[1 \mp \left(1 - \frac{2\alpha k_S}{(k_S + k_B)^2}\right)^{1/2}\right]$	$-\frac{\mathrm{ADD}\beta}{\alpha}\left[1 \mp \left(1 - \frac{\alpha^2}{\mathrm{ADD}\beta}\right)^{1/2}\right]$	$-\frac{ADD(k_B-\beta)^2}{\alpha\beta k_S}\left[1 \pm \left(1 - \frac{\alpha^2\beta K_m}{ADD(k_B-\beta)^2}\right)^{1/2}\right]$

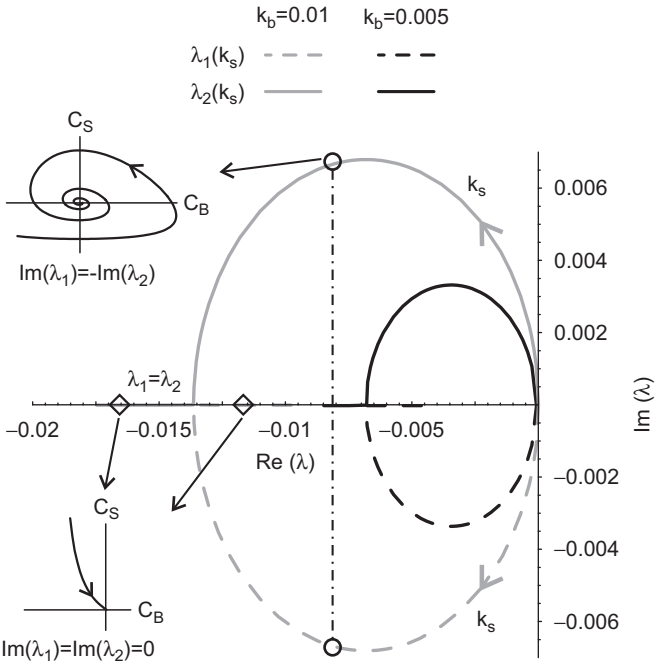

Fig. 5. Real and imaginary parts of the two eigenvalues λ_1 and λ_2 of the system of Eqs. (1) and (2) with nonlinear decomposition (Eq. (5)), as an implicit function of the decomposition rate k_S (arrows indicate increasing k_S), for two values of the biomass decay rate k_B (d^{-1}). On the left: qualitative microbe-substrate trajectories for increasing values of k_S.

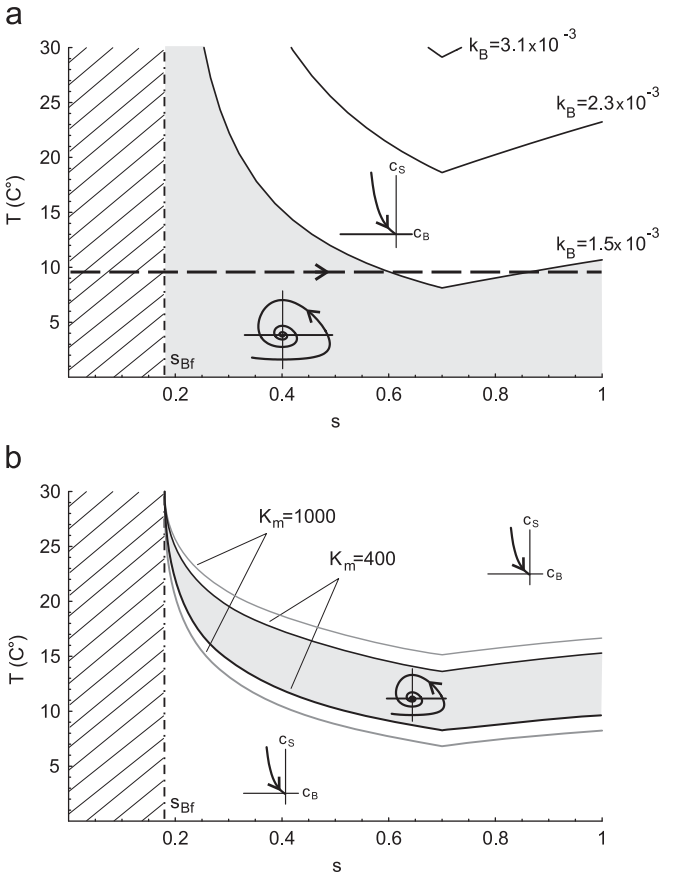

Fig. 6. Bifurcation diagrams of the system of Eqs. (1) and (2), as a function of soil moisture s and temperature T. The shaded and blank areas are regions of the parameter space corresponding to a stable focus and a stable node, respectively, while the hatched areas are not associated with any equilibrium points ($s < s_B$). (a) Multiplicative decomposition model (Eq. (5)) and effect of different values of the biomass decay rate k_B (d^{-1}). (b) Michaelis–Menten decomposition model (Eq. (4)) and role of the Michaelis constant K_m ($g\,m^{-3}$); $k_S^* = 8 \times 10^{-3}\,d^{-1}$ and $k_B = 2.3 \times 10^{-3}\,d^{-1}$ are assumed. The dot–dashed line in (a) represents a hypothetical soil moisture gradient (see text for details).

Fig. 6b illustrates the effects of the climatic factors on the nonlinear system governed by Eq. (4). Interestingly, in this case the system undergoes two bifurcations not only when soil moisture is increased (as in Fig. 6a), but also when temperature is increased, resulting in an even more complex dynamic pattern as a function of climatic parameters.

3.2. Coupled C–N dynamics

We analyze the C and N dynamics of the full system of Eqs. (8)–(12), focusing on the controls of chemical (i.e., $(C/N)_S$) and biologic (i.e., s_B and η) parameters on mineralization and immobilization regimes (Section 3.2.1) and system steady state (Section 3.2.2).

3.2.1. Controls of SOM N content and N assimilation efficiency on N-limitation conditions

The transition from net mineralization to net immobilization and from C- to N-limited conditions depends on the amount of both organic and inorganic nitrogen

available to the microbial biomass (Eqs. (16), (17) and (22)). In turn, the availability of organic N depends on the N content of the substrate (i.e., its $(C/N)_S$), and the microbial N-assimilation efficiency (η). Thus, decomposition switches from a C-limited condition when SOM is rich in organic nitrogen (low $(C/N)_S$) to a N-limited regime when SOM is N poor (high $(C/N)_S$). Hence, depending on the establishment of C- or N-limiting conditions and on the occurrence of net mineralization or net immobilization, five possible regimes of mineralization and immobilization as a function of SOM quality emerge:

- *Regime A*: no immobilization occurs due to either high N content of the substrate or high N assimilation efficiency of the microbes.
- *Regime B*: $(C/N)_S$ is higher than the incipient immobilization threshold, $(C/N)_{imm}$; thus gross immobilization is needed by the microbes to maintain their C/N ratio.
- *Regime C*: the microbial demand is further increased compared to regime B, and IMM_{pot} reaches the maximum immobilization. Although net mineralization still occurs, the system is N limited.
- *Regime D*: net immobilization is necessary to compensate the extremely low quality of the substrate, but $IMM_{pot} < IMM_{max}$, and microbial growth is still C-limited.
- *Regime E*: the compound effects of low quality substrate and low N-assimilation efficiency drive the system to conditions of net immobilization, with $IMM_{gross} = IMM_{max}$ and reduction of decomposition ($\varphi < 1$).

A detailed description of the different regimes can be obtained with reference to Figs. 7 and 8 (parameters reported in Table 1). Regime A is characterized by net mineralization and no immobilization due to high organic N availability; in this condition the system is purely mineralizing N, although MIN_{gross} decreases with $(C/N)_S$ (Fig. 7a), and DEC is C-limited (Fig. 7b). Note, however, that under the MIT hypothesis this state can not be sustained, even for an extremely N-rich substrate (i.e., $(C/N)_S \approx 0$, Fig. 8). The system remains under regime A until gross immobilization is zero. The quality threshold of incipient immobilization can be defined from Eq. (19) as

$$(C/N)_{imm} = \eta \frac{(C/N)_B}{1-r}. \quad (24)$$

Thus, clearly, the SOM quality at incipient immobilization depends on the fraction of nitrogen directly assimilated by the microbes, meaning that the higher the N assimilation efficiency, the lower the SOM N content before inducing immobilization.

Regimes B and C are both characterized by net mineralization and non-zero gross immobilization, while under regimes D and E net immobilization occurs. The quality threshold between net mineralization (regimes A–C) and net immobilization (regimes D–E), depends on $(C/N)_B$ and the microbial C assimilation efficiency, and is

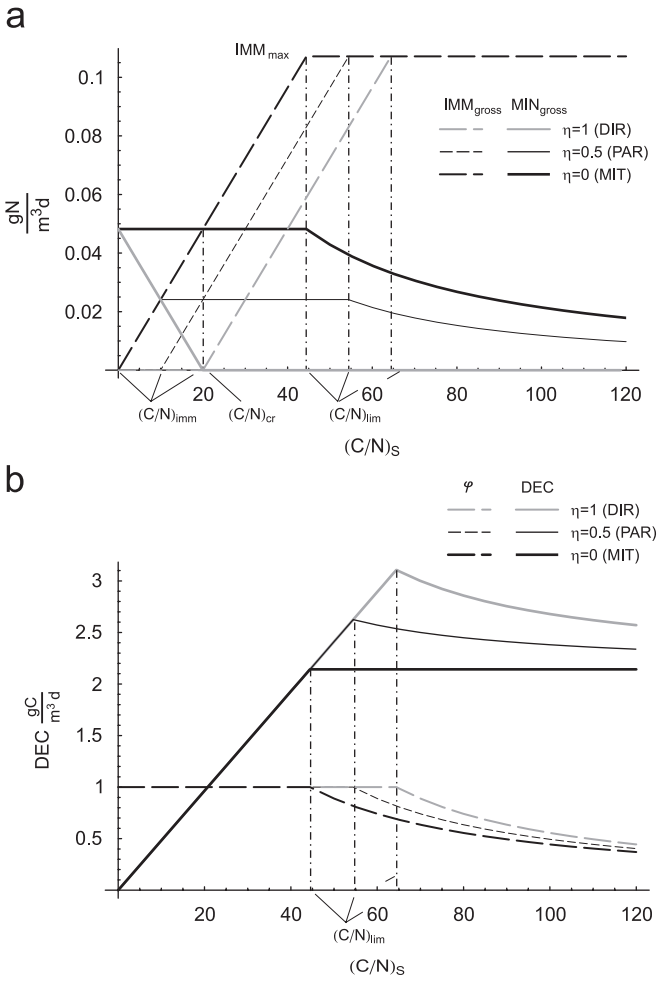

Fig. 7. Effects of SOM quality and mineralization pathways on the N cycling. (a) Gross N mineralization and immobilization; (b) decomposition and activity reduction function φ: thick gray lines refer to DIR pathway; thick black lines to MIT pathway; thin black lines to PAR pathway (for $\eta = 0.5$). The C/N ratio of the substrate is changed by increasing C_S and maintaining N_S constant.

generally referred to as critical C/N ratio of the substrate, $(C/N)_{cr}$ (Berg and Ekbohm, 1983; Bosatta and Berendse, 1984; Bosatta and Agren, 1985). In our simplified approach it can be computed imposing $MIN_{net} = 0$ (Eq. (16)),

$$(C/N)_{cr} = \frac{(C/N)_B}{1-r}. \quad (25)$$

This result, obtained with this single-compartment model, coincides with the $(C/N)_{cr}$ of the multi-compartment models by Parnas (1975) and Bosatta and Berendse (1984), and the cohort-type Q-SOIL model by Bosatta and Agren (1985). Interestingly, these two thresholds (Eqs. (24) and (25)) characterize the stoichiometry of the microbial biomass and do not depend on the rates of decomposition nor on the choice of the decomposition function (Eqs. (3)–(5)).

Under regime B, $IMM_{gross} < IMM_{max}$, while, under regime C, IMM_{gross} is restricted to IMM_{max} by low

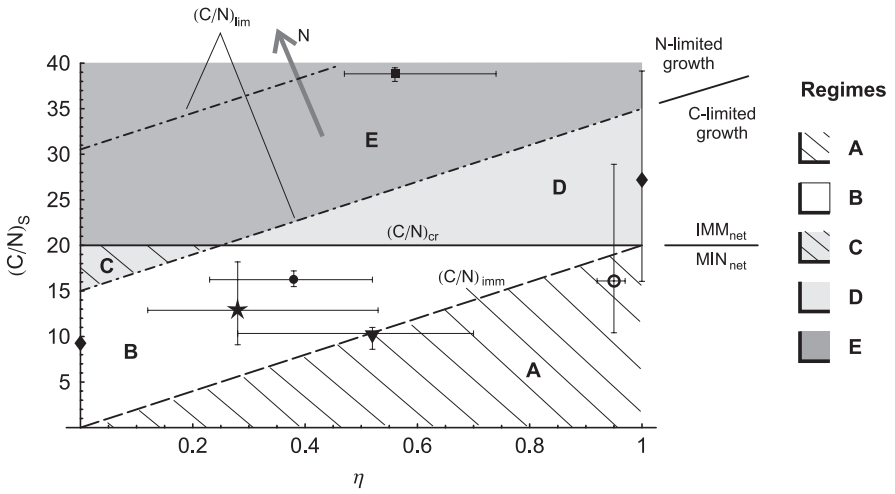

Fig. 8. Different regimes of mineralization and immobilization as a function of the quality of the substrate, $(C/N)_S$, and the N-assimilation efficiency, η (Eqs. (24)–(26)). Data points represent average measured η and $(C/N)_S$ for a number of experimental studies (bars indicate data range). η has been estimated from Eq. (27), assuming $r = 0.6$ where this parameter was not available in the original studies. Data references: ♦ Garnier et al. (2003) – CANTIS model; ○ Shi et al. (2005); ■ Recous et al. (1995), (samples R60, R80, R100; days 0-40); ▼ Hatch et al. (2000); ● Fisk and Fahey (2001); ★ Saetre and Stark (2005).

inorganic nitrogen availability (Fig. 8). The threshold between regimes B and C, $(C/N)_{lim}$, marks the onset of N limitation and separates the consumer-controlled and donor-controlled immobilization. It can be obtained by imposing $IMM_{pot} = IMM_{max}$ in Eqs. (21) and (22),

$$(C/N)_{lim} = (C/N)_{cr}\left(\eta + \frac{k_I N}{k_S N_S}\right). \quad (26)$$

For $(C/N)_S > (C/N)_{lim}$, IMM_{gross} still equals IMM_{max} (Fig. 7a), while φ decreases below one, and DEC becomes N limited (Fig. 7b; see Section 2.2.2). By adding inorganic nitrogen, $(C/N)_{lim}$ increases and the system remains in regimes A, B, and D even when decomposing low quality substrates (Fig. 8). Regimes D and E are both characterized by net immobilization, but in D the substrate quality is below $(C/N)_{lim}$ and hence it is still under C-limited conditions, while in regime *E*, $(C/N)_S > (C/N)_{lim}$ and N-limitation occurs.

Fig. 8 shows that the ranges of quality resulting in net immobilization or, more importantly, N-limitation regimes, are widened by low N assimilation efficiency, suggesting that this characteristic is an important controlling factor of soil N cycling. Under regimes B and D (when $\Phi < 0$), Eq. (18) provides a simple way to estimate η from gross mineralization and decomposition,

$$\eta = 1 - (C/N)_S \frac{MIN_{gross}}{DEC}. \quad (27)$$

Eq. (27) can be used to test the PAR hypothesis, and show that at the macroscopic level a continuum between the DIR and MIT schemes actually exists. In fact, values of η between zero and one imply that both organic N mineralization and immobilization occur simultaneously, likely as a consequence of the soil heterogeneous distribution of mineralizing and immobilizing micro-sites. Eq. (27) has thus been applied to a number of experimental datasets including both decomposition (or respiration and C utilization efficiency) and gross mineralization measures, in different environmental conditions and with a variety of soils. Reported values of gross mineralization, obtained applying the ^{15}N isotope-pool dilution technique, have been assumed representative of core scale SOM mineralization, although they might represent only small scale microbial processes (Fierer et al., 2001). The estimated values of η, along with the corresponding substrate $(C/N)_S$ are shown in Fig. 8. Most of the points lie in regimes B and D, in agreement with the assumptions of the estimation method. Exceptions are some points from Hatch et al. (2000) and Shi et al. (2006), which seem to be under regime A. In those studies, however, $(C/N)_B$ was significantly lower than eight, so that both $(C/N)_{imm}$ and $(C/N)_{cr}$ (Eqs. (24) and (25)) should be lowered for those datasets (for clarity, these modified thresholds are not represented in Fig. 8), and every point would remain under regime B. Points from Recous et al. (1995) appear to be under regime E. However, in order to avoid N-limiting conditions, the only data from their work represented in Fig. 8 are those from the samples richer in mineral N, for which a high $(C/N)_{lim}$ is expected (Eq. (26)); accordingly, also these points actually lie under regime D. Eq. (27) can also be used to interpret the results by Luxøi et al. (2006). Their regression of gross mineralization and microbial respiration can be easily recast in a form similar to Eq. (27), leading to $\eta \approx 0.6$ (assuming $r = 0.6$). Interestingly, these results span the whole range of the N assimilation efficiency, showing how N transformations in real soils are probably more complex than commonly represented in mathematical models. The heterogeneous distribution of N-rich and N-poor micro-sites (Schimel and Bennett, 2004) may cause such variability of N assimilation efficiencies at

the macroscopic scale. In fact, the MIT pathway could be a suitable model of soils with N-rich sites predominantly mineralizing N, which is then assimilated by microbial communities in N-poor sites. Analogously, the DIR pathway could represent a soil where even *N*-poor sites rely on their own organic N sources, or are poorly connected with N-rich ones. However, in real heterogeneous soils, a combination of these two extreme cases is more likely. Hence, it is not surprising that an intermediate condition suitably modeled by the PAR scheme often occurs.

3.2.2. Steady-state solution

In this section, we analyze the steady state of the system of Eqs. (8)–(12) under deterministic climatic conditions, adopting the multiplicative decomposition model (Eq. (5)) and considering a constant plant residue input to SOM. When N is not limiting and net mineralization occurs (regimes A and B), the system is able to sustain a steady state characterized by non-zero microbial biomass. On the contrary, under N-limiting conditions (regimes C, D and E) the depletion of mineral N due to intense immobilization reduces decomposition and activates a negative feedback resulting in accumulation of un-decomposed plant residues. This condition does not lead to a stable steady state, unless the N cycle is closed by including a plant submodel. In the following, the ranges of climatic (s) and biologic parameters (s_B and η) leading to stable vs. unstable states will be analyzed.

Independently of the N assimilation efficiency, the values of carbon pools at steady state (indicated with an asterisk) are the same as those already analyzed in Section 3.1 (Table 2). It is also easy to show that Eqs. (8)–(12) and Eq. (15) yield, for $s > s_w$

$$UP^* = \frac{ADD}{(C/N)_{ADD}}, \tag{28}$$

$$N^* = \frac{ADD}{(C/N)_{ADD} k_{UP}(s - s_w)}. \tag{29}$$

When immobilization does not occur (regime A), gross mineralization is simply equal to the N input in the system,

$$MIN^*_{gross} = \frac{ADD}{(C/N)_{ADD}}. \tag{30}$$

Under immobilization conditions (regime B) the steady-state gross mineralization and immobilization depend also on η. Thus, from the definitions in Eqs. (18) and (19), one can obtain

$$MIN^*_{gross} = ADD(1-\eta)\left[\frac{1-r}{r}\frac{1}{(C/N)_B} + \frac{1}{(C/N)_{ADD}}\right], \tag{31}$$

$$IMM^*_{gross} = ADD(1-\eta) \times \left[\frac{1-r}{r}\frac{1}{(C/N)_B} - \frac{\eta}{(1-\eta)}\frac{1}{(C/N)_{ADD}}\right]. \tag{32}$$

Eq. (32) clearly shows that increasing the N assimilation efficiency η causes a decrease of IMM^*_{gross}, eventually leading to a purely mineralizing system, as in Eq. (30), when $\eta > \eta_{MIN}$ (Fig. 9). On the contrary, low values of η increase immobilization, possibly up to the maximum equilibrium immobilization, as indicated by $\eta(IMM^*_{max})$, and drive the system to N-limited conditions (which however can not be sustained at equilibrium). From Eqs. (28) and (32) the threshold η_{UP} above which plant uptake is greater then gross immobilization can be easily obtained,

$$\eta_{UP} = \frac{\gamma - 1}{\gamma + 1}, \tag{33}$$

$$\gamma = \frac{1-r}{r}\frac{(C/N)_{ADD}}{(C/N)_B}. \tag{34}$$

Since $r \approx 0.6$ and in general $(C/N)_{ADD} \gg (C/N)_B$ (Table 1), $\gamma > 1$ and, from Eq. (33), $\eta_{UP} < 1$. This result at equilibrium sheds light on the role of η in plant–microbe competition (Fig. 9). When $\eta \approx 1$, no immobilization occurs and all mineralized N is taken up by plants; on the contrary, when $\eta \approx 0$, the cycling of N between microbes and the mineral N pool is more intense than plant uptake, as often found in field experiments (e.g., Schimel et al., 1989; Zak et al., 1990; Fig. 9). $\eta \approx \eta_{UP}$ might instead characterize soils where N-rich micro-sites mineralize N, which is then equally shared between plants and microbes in N-poor sites (Schimel and Bennett, 2004).

Organic N assimilation efficiency and soil moisture affect the establishment of N-limiting conditions, by controlling IMM^*_{max} and IMM^*_{gross}. Maximum immobilization at equilibrium can be obtained from Eqs. (22), (32), and C_B* (Table 2), as

$$IMM^*_{max} = \frac{(1-r)ADD^2 k_I}{r(C/N)_{ADD} k_B k_{UP}(s - s_w)}, \tag{35}$$

for $s > s_w$. Comparing Eqs. (32) and (35), one observes that for some values of soil moisture and quality of the added litter, IMM^*_{gross} may exceed IMM^*_{max}, thus establishing N-limiting conditions. The values of the quality of added litter below which the system is *C*-limited (i.e., it admits a steady state) are plotted in Fig. 10 as a function of s and η. These results can be interpreted from different perspectives. On the one hand, for a fixed value of η (i.e., assuming a certain distribution of relatively N-rich and N-poor micro-sites), we can infer from Fig. 10 that N limitation for fungi occurs only when both $(C/N)_{ADD}$ and soil moisture are very high and thus plants are strongly favored (Fig. 2). On the other hand, when $(C/N)_{ADD}$ is kept constant, the heterogeneous distribution of relatively N-rich and N-poor micro-sites plays a major role, with predominantly C-limited communities when η is high. C-limiting conditions can be thus sustained at steady state by microbial communities decomposing C-rich substrates (e.g., zymogenous microbial populations; Swift et al., 1979) when most of the micro-sites predominantly assimilates organic N (i.e., high η). This is in agreement with the results by

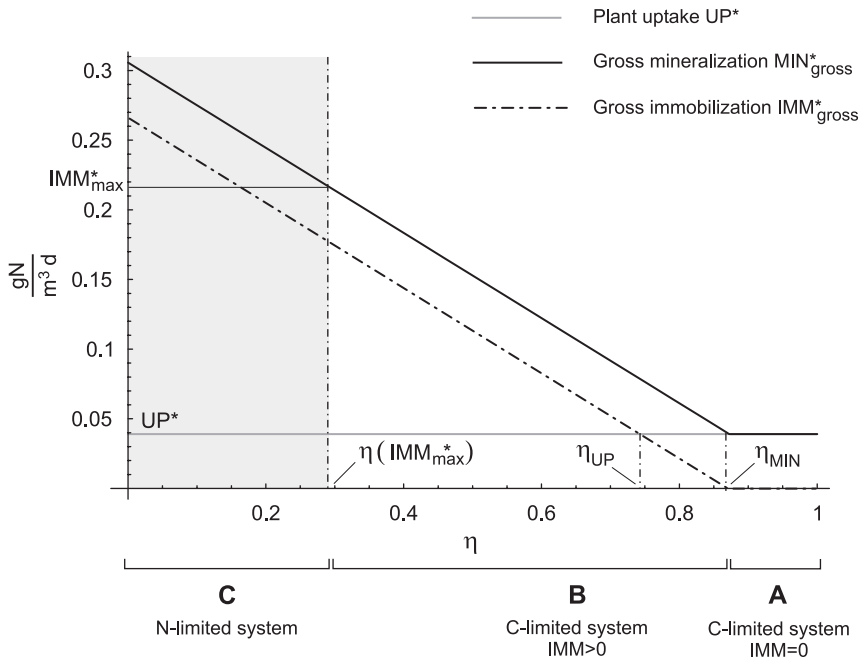

Fig. 9. Steady-state nitrogen fluxes, as a function of the organic N assimilation efficiency η (see text for details).

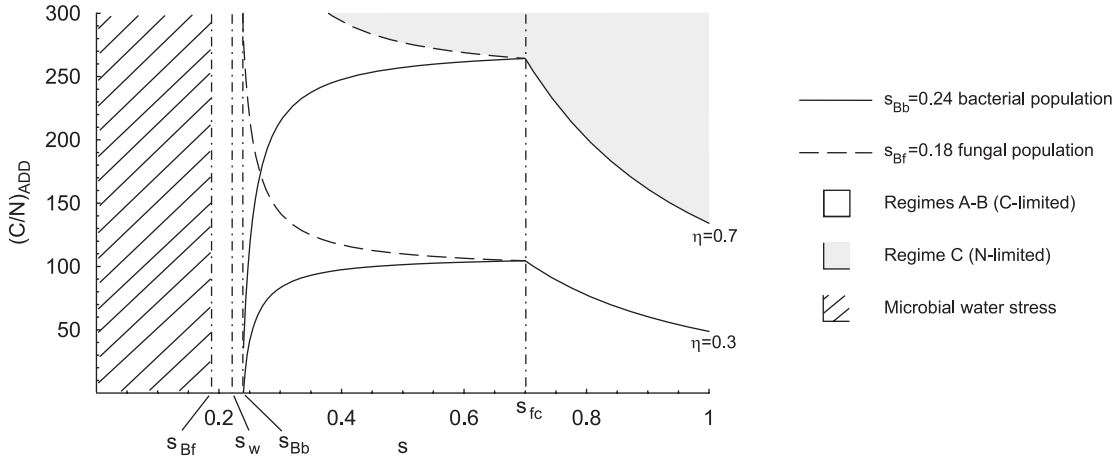

Fig. 10. Representation in the parameter space $\{s,(C/N)_{\mathrm{ADD}}\}$ of the C- or N-limiting basins for the system of Eqs. (8)–(12). Stable basins under C-limiting conditions (regimes A and B), and unstable basins under N-limiting conditions (regime C), are shown as a function of the N assimilation efficiency η and different microbial water stress points s_{B}. For clarity, the shaded and hatched areas corresponding to N-limiting conditions and water stress are only shown for the fungal community with higher η.

Hadas et al. (1992b) and Garnier et al. (2003), who modeled N cycling through these zymogenous populations using a DIR scheme. On the contrary, when the microbial population is adapted to decompose N-rich humic compounds (e.g., autochthonous populations), C-limiting conditions are maintained even if a large fraction of the N-poor micro-sites actively immobilize mineral N (i.e., low η).

In Fig. 10, the different responses of bacteria and fungi to water stress are also compared. Since fungi are often adapted to survive at water potentials that are lower than the plant wilting point and the bacterial stress points (Fig. 2; Table 1), they are competitively in advantage at low soil moisture, resulting in a sustainable steady-state decomposition even for very low N content of the substrate. This means that in soils characterized by high η and microbes adapted to water stress, the microbial biomass remains C limited even under extreme climatic conditions (s very low or close to saturation), or in the presence of nitrogen-poor substrate.

4. Conclusions

We showed the fundamental role of nonlinearities in decomposition and mineralization by means of a simplified model of soil C and N cycles. Other feedback effects taking place in soils under N-limited conditions, and not explicitly

considered here, will likely introduce further complexity in the coupled dynamics of soil C and N cycles (e.g., Schimel and Weintraub, 2003; Fog, 1988; Agren et al., 2001). Moreover, our description of plant–microbe competition is based on the classical assumption that plants mostly rely on inorganic N for their nutrition. Further investigations will explore the role of possible uptake of organic N by plants (Kaye and Hart, 1997; Schimel and Bennett, 2004).

The proposed C–N model proved suitable to analyze the basic complex relationships between microbes and their substrate and explore different N mineralization pathways. Our main conclusions can be summarized as follows:

- The comparison of different modeling approaches and experimental results in Fig. 4 clearly shows the need of modeling the nonlinear coupling between microbial biomass and its substrate to capture certain measured fluctuations. The selection of particular models remains related to the goal of the analysis as well as to the spatial and temporal scales of interest. The results of the stability analysis (Table 2) show that a linear model cannot account for fluctuating behavior resulting from strong biotic-substrate interactions. Although such tight coupling seems to be important (Fang and Moncrieff, 2005; Fang et al., 2005), evidence of fluctuations are limited to few short-term experiments in the rhizosphere (Zelenev et al., 2005b). On the long term, climatic and biotic variability, and low substrate concentrations might mask these fluctuations induced by nonlinearities. Hence, from a practical perspective, simpler linear models can be as effective as nonlinear ones to describe long-term soil C cycling (e.g., model results reported by Powlson et al., 1996). Our theoretical results suggest that fluctuations in the soil system may occur under certain environmental conditions (Fig. 6). Although presently this conclusion can not be tested with experimental results, it certainly warrants more investigation.
- The proposed coupled C–N model embeds some of the most successful features of previous multi-compartment models, accounting for the nonlinear interactions between SOM and decomposers, a flexible parameterization of the N turnover processes, and the complex nitrogen limitation feedbacks on microbial activity. Its flexibility makes it useful to analyze the role of soil and biotic parameters in the N cycles, i.e., the organic N assimilation efficiency, η, and the microbial stress point, s_B. The values of η estimated by means of Eq. (27) range between 0.1 and 0.95 (Fig. 8), clearly indicating the simultaneous occurrence of organic N assimilation and mineral N immobilization, in agreement with the PAR hypothesis. The limiting MIT and DIR model schemes thus appear to be suitable only for a restricted number of experiments. As we have shown in Fig. 9, the assumption of either DIR or MIT pathway leads respectively to underestimate or overestimate gross immobilization. Moreover, when the DIR scheme is chosen, (i.e., $\eta \gg \eta_{UP}$, see Eq. (33)), microbes are implicitly assumed to be in competitive advantage over plants for mineral N, while the smaller η (i.e., when using the MIT scheme) the higher is the N recycling between microbes and mineral N pool. Hence, biogeochemical models that do not include this variability of microbial N assimilation, and more importantly its consequences in the N balance, are likely to oversimplify the complexity of the soil N cycling.
- The contribution of water-stress adaptation to N dynamics is twofold. Under C-limiting conditions, better adaptation (low s_B) results in higher mineralization rates, and under conditions of competition for N it also provides a competitive advantage over plants and other microbes with higher s_B. As a consequence, a soil system dominated by a fungal community (with $s_{Bf} < s_w$) remains in stable C-limited conditions even when fed with N-poor inputs. On the contrary, under low soil moisture conditions, the depletion of N by plants couples with reduced activity of bacteria (with $s_{Bb} < s_w$), that cannot replenish the mineral N pool, and leads towards conditions of strong N-limitation.

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References

Agren, G.I., Bosatta, E., Magill, A.H., 2001. Combining theory and experiment to understand effects of inorganic nitrogen on litter decomposition. Oecologia 128, 94–98.

Andrén, O., Paustian, K., 1987. Barley straw decomposition in the field: a comparison of models. Ecology 68 (5), 1190–1200.

Argyris, J., Faust, G., Haase, M., 1994. An Exploration of Chaos. North Holland, Amsterdam, 751pp.

Baisden, W.T., Amundson, R., 2003. An analytical approach to ecosystem biogeochemistry modeling. Ecological Applications 13 (3), 649–663.

Barak, P., Molina, J.A.E., Hadas, A., Clapp, C.E., 1990. Mineralization of amino acids and evidence of direct assimilation of organic nitrogen. Soil Science Society of America Journal 54, 769–774.

Barraclough, D., 1997. The direct or MIT route for nitrogen immobilization: a ^{15}N mirror image study with leucine and glycine. Soil Biology & Biochemistry 29 (1), 101–108.

Benbi, D.K., Richter, J., 2002. A critical review of some approaches to modelling nitrogen mineralization. Biology and Fertility of Soils 35, 168–183.

Berg, B., Ekbohm, G., 1983. Nitrogen immobilization in decomposing needle litter at variable carbon:nitrgen ratios. Ecology 64 (1), 63–67.

Blagodatsky, S.A., Richter, O., 1998. Microbial growth in soil and nitrogen turnover: a theoretical model considering the activity state of microorganisms. Soil Biology & Biochemistry 30 (13), 1743–1755.

Bolker, B.J., Pakala, S.W., Parton, W.J., 1998. Linear analysis of soil decomposition: insights from the century model. Ecological Applications 8 (2), 425–439.

Bosatta, E., Agren, G.I., 1985. Theoretical analysis of decomposition of heterogeneous substrates. Soil Biology & Biochemistry 17 (5), 601–610.

Bosatta, E., Agren, G.I., 1994. Theoretical analysis of microbial biomass dynamics in soils. Soil Biology & Biochemistry 26 (1), 143–148.

Bosatta, E., Berendse, F., 1984. Energy or nutrient regulation of decomposition: implications for mineralization–immobilization response to perturbations. Soil Biology & Biochemistry 16 (1), 63–67.

Brady, N.C., Weil, R.R., 1996. The Nature and Properties of Soil, 11th ed. Prentice Hall, Upper Saddle River, NJ.

Clarke, A.L., Barley, K.P., 1968. The uptake of nitrogen from soils in relation to solute diffusion. Australian Journal of Soil Research 6, 75–92.

de Willigen, P., 1991. Nitrogen turnover in the soil-crop system; comparison of fourteen simulation models. Fertilizer Research 27, 141–149.

D'Odorico, P., Laio, F., Porporato, A., Rodriguez-Iturbe, I., 2003. Hydrologic control on soil carbon and nitrogen cycles II a case study. Advances in Water Resources 26, 59–70.

Drury, C.F., Voroney, R.P., Beauchamp, E.G., 1991. Availability of NH_4^+–N to microorganisms and the internal N cycle. Soil Biology & Biochemistry 23 (2), 165–169.

Fang, C., Moncrieff, J.B., 2005. The variation of soil microbial respiration with depth in relation to soil carbon composition. Plant and Soil 268, 243–253.

Fang, C., Smith, P., Smith, J.U., Moncrieff, J.B., 2005. Incorporating microorganisms as decomposers into models to simulate soil organic matter decomposition. Geoderma 129, 139–146.

Fierer, N., Schimel, P.J., Catex, R.G., Zou, J., 2001. Influence of balsam poplar tannin fractions on carbon and nitrogen dynamics in Alaskan taiga floodplain soils. Soil Biology & Biochemistry 33, 1827–1839.

Finzi, A.C., DeLucia, E.H., Hamilton, J.G., Richter, D.D., Schlesinger, W.H., 2002. The nitrogen budget of a pine forest under free CO_2 enrichment. Oecologia 132, 567–578.

Fisk, M.C., Fahey, T.J., 2001. Microbial biomass and nitrogen cycling responses to fertilization and litter removal in young northern hardwood forests. Biogeochemistry 53, 201–223.

Fog, K., 1988. The effect of added nitrogen on the rate of decomposition of organic matter. Biologial Review 63, 433–462.

Freckman, D.W., 1986. The ecology of dehydration in soil organisms. In: Leopold, A.C. (Ed.), Membranes, Metabolism and Dry Organisms. Cornell University Press, Ithaca, pp. 157–168.

Garnier, P., Néen, C., Mary, B., Lafolie, F., 2001. Evaluation of a nitrogen transport and transformation model in a bare soil. European Journal of Soil Science 52, 253–268.

Garnier, P., Néen, C., Aita, C., Recous, S., Lafolie, F., Mary, B., 2003. Modelling carbon and nitrogen dynamics in a bare soil with and without straw incorporation. European Journal of Soil Science 54, 555–568.

Griffin, D.M., 1980. Water potential as a selective factor in the microbial ecology of soils. In: SSSA Special Publication 9, Water Potential Relations in Soil Microbiology. Soil Science Society of America, Madison, WI, pp. 141–151.

Gusman, A.J., Marino, M.A., 1999. Analytical modeling of nitrogen dynamics in soils and ground water. Journal of Irrigation and Drainage Engineering 125 (6), 330–337.

Hacke, U.G., Sperry, J.S., Ewers, B.E., Ellsworth, D.S., Schafer, K.V.R., Oren, R., 2000. Influence of soil porosity on water use in pinus Taeda. Oecologia 124, 495–505.

Hadas, A., Molina, J.A.E., Feigenbaum, S., Clapp, C.E., 1987. Simulation of nitrogen-15 immobilization by the model NCSOIL. Soil Society of America Journal 51, 102–106.

Hadas, A., Molina, J.A.E., Feigenbaum, S., Clapp, C.E., 1992a. Factors affecting nitrogen immobilization in soil as estimates by simulation models. Soil Society of America Journal 56, 1481–1486.

Hadas, A., Sofer, M., Molina, J.A.E., Barak, P., Clapp, C.E., 1992b. Assimilation of nitrogen by soil microbial population: NH_4 versus organic N. Soil Biology & Biochemistry 24 (2), 137–143.

Hansen, S., Jensen, L.S., Nielsen, N.E., Svendsen, H., 1991. Simulation of nitrogen dynamics and biomass production in winter wheat using the Danish simulation model DAISY. Fertilizer Research 27, 245–259.

Hansen, S., Jensen, H.E., Shaffer, M.J., 1995. Developments in modeling nitrogen transformation in soils. In: Bacon, P.E. (Ed.), Nitrogen Fertilization in the Environment. Marcel Dekker Inc., New York, NW.

Hart, S.C., Nason, G.E., Myrold, D.D., Perry, D.A., 1994. Dynamics of gross nitrogen transformations in an old growth forest: the carbon connection. Ecology 75 (4), 880–891.

Harte, J., Kinzig, A.K., 1993. Mutualism and competition between plants and decomposers: implications for nutrient allocations in ecosystems. The American Naturalist 141 (6), 829–846.

Hatch, D.J., Lovell, R.D., Antil, R.S., Jarvis, S.C., Owen, P.M., 2000. Nitrogen mineralization and microbial activity in permanent pastures amended with nitrogen fertilizer or dung. Biology and Fertility of Soils 30, 288–293.

Jansson, S.L., 1958. Tracer studies on nitrogen transformations in soils with special attention to mineralization–immobilization relationships. Annals of the Royal Agriculture College of Sweden 24, 105–361.

Katterer, T., Andrén, O., 2001. The ICBM family of analytically solved models of soil carbon, nitrogen and microbial biomass dynamics—description and application examples. Ecological Modelling 136, 191–207.

Kaye, J.P., Hart, S.C., 1997. Competition for nitrogen between plants and soil microorganisms. Trends in Ecology and Evolution 12, 139–143.

Laio, F., Porporato, A., Ridolfi, L., Rodriguez-Iturbe, I., 2001. Plants in water-controlled ecosystems. Active role in hydrological processes and response to water stress. II Probabilistic soil moisture dynamics. Advances in Water Resources 24 (7), 707–723.

Luxøi, J., Brunn, S., Stenberg, B., Breland, T.A., Jensen, L.S., 2006. Prediction of gross and net mineralization–immobilization-turnover from respiration. Soil Science Society of America Journal 70, 1121–1128.

Manzoni, S., Porporato, A., D'Odorico, P., Laio, F., Rodriguez-Iturbe, I., 2004. Soil nutrient cycles as a nonlinear dynamical system. Nonlinear Processes in Geophysics 11, 589–598.

Mary, B., Recous, S., Darwis, D., Robin, D., 1996. Interactions between decomposition of plant residues and nitrogen cycling in soil. Plant and Soil 181, 71–82.

Mary, B., Recous, S., Robin, D., 1998. A model for calculating nitrogen fluxes in soil using ^{15}N tracing. Soil Biology & Biochemistry 30 (14), 1963–1979.

McGill, W.B., 1996. Review and classification of ten soil organic matter (SOM) models. In: Powlson, D.S., Smith, P., Smith, J.U. (Eds.), Evaluation of Soil Organic Matter Models. Using Existing Long Term Datasets. NATO ASI Series, Series I: Global Environmental Change, Vol. 38, pp. 111–132.

McGill, W.B., Hunt, H.W., Woodmansee, R.G., Reuss, J.O., 1981. PHOENIX, a model of the dynamics of carbon and nitrogen in grassland soils. In: Clark, F.E., Rosswall, T. (Eds.), Terrestrial Nitrogen Cycles. Ecological Bullettin No. 33, Stockholm, pp. 49–115.

Molina, J.A.E., Smith, P., 1998. Modeling carbon and nitrogen processes in soils. Advances in Agronomy 62, 253–298.

Molina, J.A.E., Clapp, C.E., Shaffer, M.J., Chichester, F.W., Larson, W.E., 1983. NCSOIL, a model of nitrogen and carbon transformations in soils: description, calibration and behavior. Soil Science Society of America Journal 47, 85–91.

Murray, J.D., 2002. Mathematical Biology. I. An Introduction, third ed. Springer, Berlin, 551pp.

Neill, C., Gignoux, J., 2006. Soil organic matter decomposition driven by microbial growth: a simple model for a complex network of interactions. Soil Biology & Biochemistry 38, 803–811.

Panikov, N.S., Sizova, M.V., 1996. A kinetic method for estimating the biomass of microbial functional groups in soil. Journal of Microbiological Methods 24, 219–230.

Parnas, H., 1975. Model for decomposition of organic material by microorganisms. Soil Biology & Biochemistry 7, 161–169.

Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal 51, 1173–1179.

Paustian, K., 1994. Modelling soil biology and biochemical processes for sustainable agriculture research. In: Pankhurst, Z.E., Doube, B.M., Gupta, V.V.S.R., Grace, P.R. (Eds.), (Eds), Soil Biota. Management in Sustainable Farming Systems. CSIRO Information Service, Melbourne, Australia.

Porporato, A., D'Odorico, P., Laio, F., Rodriguez-Iturbe, I., 2003. Hydrologic controls on Soil carbon and nitrogen cycle I: Modelling scheme. Advances in Water Resources 26, 45–58.

Powlson, D.S., Smith, P., Smith, J.U. (Eds.), 1996. Evaluation of Soil Organic Matter Models. Using Existing Long Term Database. NATO ASI Series. Series I: Global Environmental Change 38. Springer, Berlin, New York, 429pp.

Ratkowsky, D.A., Olley, J., McMeekin, T.A., Ball, A., 1982. Relationship between temperature and growth rate of bacterial cultures. Journal of Bacteriology 149 (1), 1–5.

Recous, S., Robin, D., Darwis, D., Mary, B., 1995. Soil inorganic N availability: effect on maize residue decomposition. Soil Biology & Biochemistry 27 (12), 1529–1538.

Rodrigo, A., Recous, S., Neel, C., Mary, B., 1997. Modelling temperature and moisture effects on C–N transformations in soils: comparison of nine models. Ecological Modelling 102, 325–339.

Saetre, P., Stark, J.M., 2005. Microbial dynamics and carbon and nitrogen cycling following re-wetting of soils beneath two semi-arid plant species. Oecologia 142, 247–260.

Schimel, J.P., Bennett, J., 2004. Nitrogen mineralization: challenges of a changing paradigm. Ecology 85 (3), 591–602.

Schimel, J.P., Weintraub, M.N., 2003. The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. Soil Biology & Biochemistry 35 (4), 549–563.

Schimel, J.P., Jackson, L.E., Firestone, M.K., 1989. Spatial and temporal effects on plant–microbial competition for inorganic nitrogen in a California annual grassland. Soil Biology & Biochemistry 21 (8), 1059–1066.

Schjonning, P., Thomsen, I.K., Moldrup, P., Christensen, B.T., 2003. Linking soil microbial activity to water- and air-phase contents and diffusivities. Soil Society of America Journal 67, 156–165.

Schwinning, S., Sala, O.E., 2004. Hierarchy of responses to resource pulses in arid and semiarid ecosystems. Oecologia 141, 211–220.

Semenov, A.M., van Bruggen, A.H.C., Zelenev, V.V., 1999. Moving waves of bacterial populations and total organic carbon along roots of wheat. Microbial Ecology 37, 116–128.

Shi, W., Yao, H.Y., Bowman, D., 2006. Soil microbial biomass, activity and nitrogen transformations in a turfgrass chronosequence. Soil Biology & Biochemistry 38, 311–319.

Skopp, J., Jawson, M.D., Doran, J.W., 1990. Steady-state aerobic activity as a function of soil water content. Soil Science Society of American Journal 54, 1619–1625.

Smith, P., Smith, J.U., Powlson, D.S., McGill, W.B., Arah, J.R.M., Chertov, O.G., Coleman, K., Franko, U., Frolking, S., Jenkinson, D.S., Jensen, L.S., Kelly, R.H., Klein-Gunnewiek, H., Komarov, A.S., Li, C., Molina, J.A.E., Mueller, T., Parton, W.J., Thornley, J.H.M., Whitmore, A.P., 1997. A comparison of the performance of nine soil organic matter models using datasets from seven long-term experiments. Geoderma 81 (1–2), 153–225.

Smith, P., Andrén, O., Brussaard, L., Dangerfield, M., Ekschmitt, K., Lavelle, P., Tate, K., 1998. Soil biota and global change at the ecosystem level: describing soil biota in mathematical models. Global Change Biology 4, 773–784.

Stark, J.M., Firestone, M.K., 1995. Mechanisms for soil moisture effects on activity of nitrifying bacteria. Applied and Environmental Microbiology 61 (1), 218–221.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. Studies in Ecology, Vol. 5. University of California Press, Berkeley, Los Angeles, CA.

Van Veen, J.A., Ladd, J.N., Amato, M., 1985. Turnover of carbon and nitrogen through the microbial biomass in a sandy loam and a clay soil incubated with [^{14}C(U)]glucose and [^{15}N]$(NH_4)_2SO_4$ under different moisture regimes. Soil Biology & Biochemistry 17 (6), 747–756.

VEMAP Members, 1995. Vegetation ecosystem modeling and analysis project—comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO_2 doubling. Global Biogeochemical Cycles 9 (4), 407–437.

Vinolas, L.C., Healey, J.R., Jones, D.L., 2001. Kinetics of soil microbial uptake of free amino acids. Biology and Fertility of Soils 33, 67–74.

Whitmore, A.P., 1996a. Describing the mineralization of carbon added to soil in crop residues using second-order kinetics. Soil Biology & Biochemistry 28 (10–11), 1435–1442.

Whitmore, A.P., 1996b. Alternative kinetic laws to describe the turnover of the microbial biomass. Plant and Soil 181, 169–173.

Wu, L., McGechan, M.B., 1998. A review of carbon and nitrogen processes in four soil nitrogen dynamics models. Journal of Agricultural Engineering Research 69, 279–305.

Zak, D.R., Groffman, P.M., Pregitzer, K.S., Christensen, S., Tiedje, J.M., 1990. The vernal dam: plant–microbe competition for nitrogen in northern hardwood forests. Ecology 7 (12), 651–656.

Zak, D.R., Holmes, W.E., MacDonald, N.W., Pregitzer, K.S., 1999. Soil temperature, matric potential, and the kinetics of microbial respiration and nitrogen mineralization. Soil Society of America Journal 63, 575–584.

Zelenev, V.V., van Bruggen, A.H.C., Semenov, A.M., 2000. "BACWAVE," a spatial–temporal model for traveling waves of bacterial populations in response to a moving carbon source in soil. Microbial Ecology 40, 260–272.

Zelenev, V.V., van Bruggen, A.H.C., Semenov, A.M., 2005a. Modeling wave-like dynamics of oligotrophic and copiotrophic bacteria along wheat roots in response to nutrient input from a growing root tip. Ecological Modelling 188, 404–417.

Zelenev, V.V., van Bruggen, A.H.C., Semenov, A.M., 2005b. Short-term wavelike dynamics of bacterial populations in response to nutrient input from fresh plant residues. Microbial Ecology 49, 83–93.