

Hydrologic controls on soil carbon and nitrogen cycles.

I. Modeling scheme

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Abstract

The influence of soil moisture dynamics on soil carbon and nitrogen cycles is analyzed by coupling an existing stochastic soil moisture model [Adv. Water Resour. 24 (7) (2001) 707; Proc. R. Soc. Lond. A 455 (1999) 3789] to a system of eight nonlinear differential equations that describe the temporal evolution of the organic matter and the mineral nitrogen in the soil at the daily to seasonal time scales. Special attention is devoted to the modeling of the soil moisture control on mineralization and immobilization fluxes, leaching losses, and plant nitrogen uptake, as well as to the role played by the soil organic matter carbon-to-nitrogen ratio in determining mineralization and immobilization. The model allows a detailed analysis of the soil nitrogen cycle as driven by fluctuations in soil moisture at the daily time scale resulting from the stochastic rainfall variability. The complex ensuing dynamics are studied in detail in a companion paper [Adv. Water Resour. 26 (1) (2003) 59], which presents an application to the Nylsvley savanna in South Africa. The model accounts for the soil moisture control on different components of the nitrogen cycle on a wide range of time scales: from the high frequency variability of leaching and uptake due to the nitrate flushes after persistent rainfall following a period of drought, to the low frequency temporal dynamics of the soil organic matter pools. All the fluctuations in the various pools are statistically characterized in relation to their dependence on climate, soil, and vegetation characteristics.

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1. Introduction

Hydrologic controls on the dynamics of water-controlled ecosystems are manifold, and range from the role of soil moisture in plant water stress [26] to its effects on the various components of soil nutrient cycles [30]. Since plants in water-controlled ecosystems are often both water and nutrient limited, it is difficult—if not impossible—to separate the extent to which net primary production is controlled by water or nutrient availability. Water deficit heavily contributes to nutrient deficit through a series of different mechanisms, so that an understanding of plant stress requires the joint analysis of water and nutrient cycles. As noticed by Pastor et al. [24], the nitrogen cycle needs to be explained through the water balance. The latter depends on the type of plant which, in turn, determines litter composition.

Although the importance of the interaction between nutrient-cycles and hydrology has been recognized for a

long time, its consequences are far from being completely understood. Soil moisture, which is itself the result of the joint action of climate soil and vegetation, controls the soil carbon and nitrogen cycles both directly and indirectly: directly, it impacts some of the most important phases of these cycles, such as decomposition, leaching, and plant uptake; indirectly, through its influence on vegetation growth, soil moisture affects the amount and composition of plant residues. The presence of different interacting processes with several nonlinearities and feedbacks makes the whole picture quite complex (Fig. 1). In this analysis we only focus on the direct influence of soil moisture on the soil carbon and nitrogen cycles, using field data to assign the plant characteristics required by the model (e.g., flux of added litter, rooting depth, water and nitrogen uptake, etc.). The use of fixed vegetation characteristics allows us to concentrate on the soil system, without modeling the part of the carbon and nitrogen cycles that is related to vegetation growth. Nevertheless, this simplification does not represent a real limitation of the model because vegetation parameters may be expressed as dependent on time; the assumption of fixed vegetation characteristics is just a

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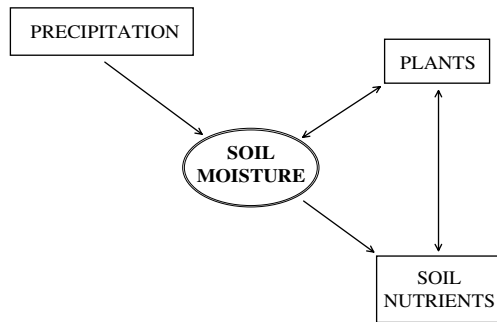


Fig. 1. Central role of soil moisture in the soil–plant system.

convenient approach to initially avoid further complications and uncertainties that arise from the use of vegetation-growth models.

The investigation of the role of soil moisture dynamics on the carbon and nitrogen cycles has mainly originated from agricultural and ecological studies. Field and laboratory experiments were followed by quantitative modeling [2,6,17,31,32,38,39]. Pastor and Post [25] and Post and Pastor [28] investigated the influence of climate, soil moisture, and vegetation on carbon and nitrogen cycles in natural ecosystems. They found that soil moisture limitation increased with the water holding capacity along a soil texture gradient and that low water availability altered the composition of the tree species and, in turn, the nitrogen availability. Parton and coworkers [21–23,33,34] noticed a correlation between water and nitrogen limitations due to the water budget control of carbon and nitrogen fluxes. They also showed that, whereas biophysical systems may have a memory of one or two years through the soil moisture storage, the linkage of water, carbon, and nitrogen cycles can induce lagged effects over decades through the decomposition of soil organic matter (SOM).

Other studies have investigated the effect of climate and hydrology on SOM and nutrients [3,4,11,15,19,27], pointing out the importance of quantitative modeling in the analysis of the physical processes in the soil–nutrient system. Moorhead et al. [19] and Bolker et al. [5] have emphasized the need for greater temporal resolution in the modeling of climate and litter-quality controls (most models work at the monthly time scale), as well as the need for a finer-scale description of the relationships between carbon and nitrogen dynamics during decomposition.

Soil moisture has an impact on soil carbon and nitrogen cycles at different time scales through the processes of mineralization, leaching, plant uptake, and denitrification. By enhancing some processes and quenching others, the temporal patterns of soil moisture can regulate the sequence of fluxes between different pools and determine the temporal dynamics of the other state

variables of the system. As shown in the application of the model [8], the statistically-steady fluctuations of soil moisture, at the daily time scale, are by themselves capable of giving rise to rich temporal dynamics in the soil carbon and nitrogen cycles, featuring slow accumulation of SOM and bacterial growth, flushes of mineral nitrogen availability for plant uptake, and rapid and intermittent leaching events. Since most of the phases of the cycles are closely interconnected, a mathematical model is the necessary initial step for a probabilistic analysis of the fluctuations within the various carbon and nitrogen cycle pools and their dependence on climate, soil, and vegetation characteristics.

In this paper the probabilistic model for soil moisture dynamics proposed by Rodriguez-Iturbe et al. [29] and Laio et al. [16] is coupled to a system of equations describing the temporal dynamics of carbon and nitrogen over the depth of active soil. The analytical formulation of soil moisture dynamics at the daily time scale accounts for the rainfall stochastic structure and the key soil and vegetation characteristics and provides the basis for the investigation of the hydrologic control on the various components of the soil nitrogen cycle. The SOM and mineral nitrogen are described by five pools that represent litter, biomass, humus, ammonium, and nitrate. Particular attention is devoted to the modeling of mineralization and immobilization, as controlled by the soil moisture level and by the soil organic matter carbon-to-nitrogen (C/N) ratio, as well as to plant uptake and leaching. Since interest is here mainly in water-controlled ecosystems, where fluctuations in soil moisture rather than temperature are crucial [10,35], the present formulation considers isothermal conditions, even though the effect of temperature can easily be added, either by directly using measured temperature time series as part of the input or by coupling the model with equations that describe the thermal balance of the active soil layer. Likewise, only the most important fluxes in the soil nitrogen cycle are incorporated into the model to facilitate the interpretation of the resulting dynamics.

The paper is organized as follows. After a brief description of the carbon and nitrogen cycles in the soil (Section 2), the probabilistic soil moisture model of Rodriguez-Iturbe et al. [29] and Laio et al. [16] is briefly reviewed in Section 3. The core of the paper is Section 4, where a detailed description of the analytical model for the carbon and nitrogen dynamics is presented. Finally, conclusions are drawn and directions for further research are given in Section 5. A companion paper [8] presents an application of the model to the Nylsvley savanna in South Africa [35]; the data available on this ecosystem [35] allow an adequate testing of the model. The properties of the nitrogen and carbon dynamics at this site are simulated and how the random fluctuations imposed by the stochastic forcing of precipitation

propagate to the state variables of the system is studied in detail.

2. The carbon and nitrogen cycles in soils

2.1. Soil organic matter and carbon cycle

Fig. 2 shows the carbon cycle within the soil–plant–atmosphere system. Although it is only a small portion of the global carbon cycle, this portion of the carbon and nitrogen cycles has high circulation rates which make it almost a closed cycle. Globally, the soil contains more carbon than the vegetation and atmospheric pools combined. Plants take carbon from the atmosphere through photosynthesis; part of it is used by plants as a source of energy and then directly released by respiration, while another part is assimilated by vegetation and later transferred as plant litter to the soil, where it becomes part of the SOM. This is a complex and varied mixture of organic substances, with three main components: plant residues, microorganisms biomass, and humus (Fig. 3). Soil moisture has an important long-term influence on the amount and quality of litter, especially on its carbon-to-nitrogen (C/N) ratio which in turn affects the rates of SOM decomposition. Both the amount of added litter and its C/N ratio are considered as an external input to the system and their values are estimated from field data. This is a simplification which allows us to investigate the basic mechanisms of the soil carbon and nitrogen cycles, without directly linking these mechanisms to plant growth, as would be required in other types of analysis concerning the long-term dynamics of plant ecosystems.

SOM decomposition, or mineralization, involves enzymatic oxidation which produces mineral compounds (e.g. ammonium) and carbon dioxide (CO₂), that is then

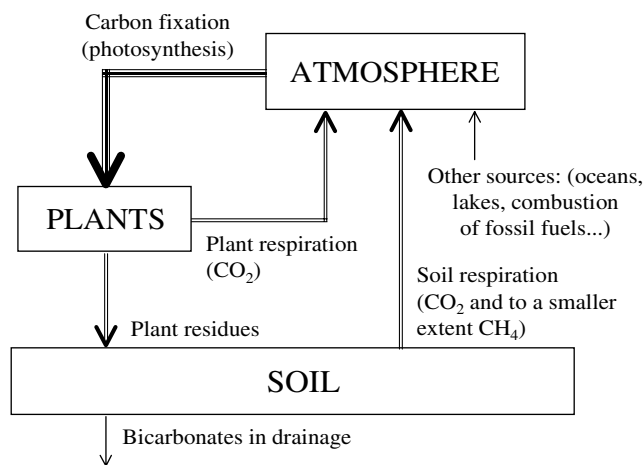


Fig. 2. A simplified representation of the soil–plant–atmosphere carbon cycle (the thickness of the arrows and the dimension of the rectangles indicate the relative importance of the relevant fluxes or pools).

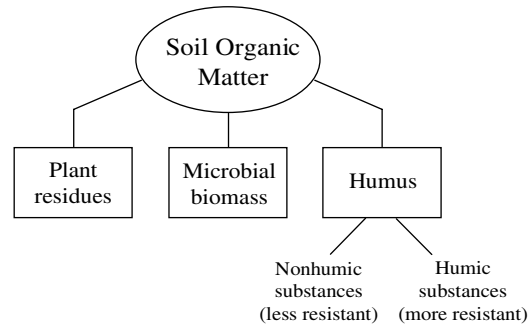


Fig. 3. Scheme of the three main SOM components, redrawn after Brady and Weil [6].

returned to the atmosphere (soil respiration). While part of the carbon is lost as soil respiration and the simpler compounds are metabolized by soil microbes, the most complex ones are not metabolized but, along with other compounds polymerized by soil microbes, combine to form the so-called humic substances, or resistant humus (Fig. 3). In soils of mature natural ecosystems the release of carbon as CO₂ is generally balanced in the long term by the input of plant residues, while at shorter time scales (e.g. seasonal-to-interannual) the carbon content is subject to fluctuations induced by climatic and hydrologic variability, so that the entire soil carbon cycle is quite sensitive to external disturbances.

The decomposition process is related to immobilization in a complex manner and is regulated by the SOM carbon-to-nitrogen (C/N) ratio and by the environmental conditions. It is usually modeled as first order kinetics (i.e. proportional to the amount of substance to be decomposed and to the amount of existing decomposing bacteria). When plant residues are added to the soil and the conditions are favorable, the bacterial colonies grow fast, but as soon as the decomposable SOM is reduced, they starve and die as easily. The decomposition of dead microbial cells is associated with the release of simple products, such as nitrate and sulphates. Different bacterial colonies exist, each specialized in a given part of the decomposition process. Such bacteria are very sensitive to environmental conditions and, in particular, to soil water potential [10]. This in great part determines the close relationship between mineralization and soil moisture that is to be discussed in the following sections.

Since most of the organic residues are deposited and incorporated at the surface, SOM tends to accumulate in the upper layers of the soils. In general, under similar climatic conditions, total SOM is higher and vertically more uniform in soils under grasslands than under forests. A relatively high proportion of plant residues in grasslands consists of root matter, which decomposes more slowly and contributes more effectively to soil humus than does forest litter. Other ecosystems with

deeper-rooted plants, such as the Nylsvley savanna that is considered in the application paper [8], also tend to have a uniform distribution of SOM and mineral nitrogen over the whole root layer (except perhaps for the most superficial layer). This reduces the importance of the vertical dimension in the modeling of the carbon and nitrogen dynamics and allows us to use the same vertical domain (i.e. the so-called active soil depth or rooting depth Z_r) which is used for soil moisture dynamics and the water balance.

2.2. Soil nitrogen cycle

Although it is an essential nutrient for plants, soil nitrogen exists mostly in the form of organic compounds that protect it from loss but leave it largely unavailable to vegetation. Plants almost only uptake mineral nitrogen, in the form of ammonium (NH_4^+) and nitrate (NO_3^-), that are made available through SOM decomposition. For this reason, the nitrogen cycle is closely linked to that of carbon. Fig. 4 provides a schematic representation of the main component of the nitrogen cycle in soils. The existence of an internal cycle is clear. This involves only soil and plants through nitrogen uptake and the production of SOM and dominates the nitrogen turnover at the daily-to-seasonal time scales. The other external fluxes, such as wet and dry deposition and the biological fixation, become important only in the long-term balance and are neglected in this analysis.

For the nitrogen cycle, the decomposition of SOM gives rise to ammonia and nitrate (ammonification and nitrification); $\approx 1.5\text{--}3.5\%$ of the organic nitrogen of a soil mineralizes annually, depending on environmental factors, such as pH, temperature, and soil moisture. The

influence of soil moisture on mineralization is mainly due to the balance between aeration which diminishes with soil moisture and favorable humid conditions for microbial biomass (Fig. 5). At high soil moisture levels, anoxic conditions prevent bacteria from performing the aerobic oxidation that is necessary for decomposition. The reason for the reduction of the decomposition rate at low soil moisture levels is twofold [10,37]. Firstly, a lack of substrate supply due to the reduced water content reduces microbial activity; as the pores within solid matrices dry and the water film coating the surfaces becomes thinner, diffusion path lengths become more tortuous and the rate of substrate diffusion to microbial cells declines. Secondly, low water contents induce low soil water potentials which lower intracellular water potential and, in turn, reduce hydration and the activity of enzymes. Interestingly, as far as this second aspect is concerned, the water stress of soil microbes has similar characteristics to plant water stress [26]. In water-controlled ecosystems, which are the main focus of our investigation, temperature is usually less important than soil moisture, especially at the daily time scale. The most favorable conditions for mineralization are found around $20\text{--}30^\circ\text{C}$; mineralization practically ceases outside the $5\text{--}50^\circ\text{C}$ temperature range and also tends to decline in acid soils [6].

When the conditions are favorable nitrification is quite rapid. In hot and dry environments, sudden water availability can cause a flush of soil nitrate production, which may greatly influence the growth patterns of natural vegetation [8]. For this reason, under warm and hot conditions, nitrate is the predominant form of nitrogen in most soils. Release of ammonia gas (NH_3) may be of certain importance (ammonia volatilization), especially in drying and hot sandy soils with ammonium accumulation in the top layers. The presence of nitrite (NO_2^-), instead, is always negligible, as its transformation to NO_3^- is practically immediate. This is important, since NO_2^- is quite toxic.

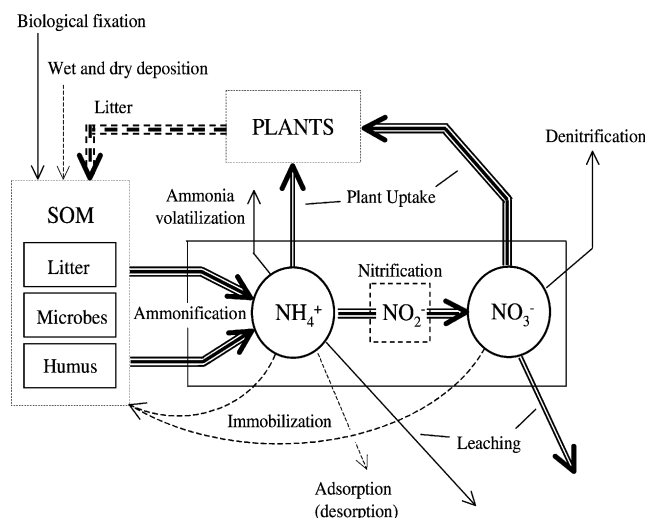


Fig. 4. Schematic representation of the soil nitrogen cycle (the dimension of the arrows indicates the relative importance of the various fluxes in the cycle; the continuous lines refer to processes wherein the impact of soil moisture is more relevant).

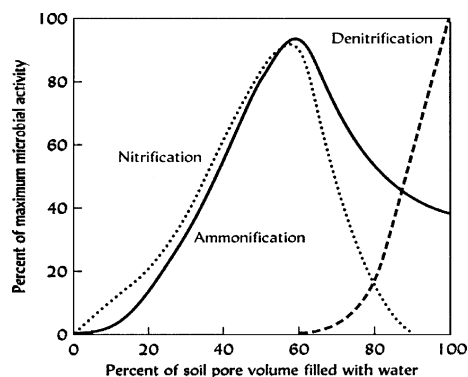


Fig. 5. Rate of microbial activity related to the various phases of nitrogen transformation as a function of the soil water content; after Brady and Weil [6].

As already mentioned, the mineralization rate also depends on the composition of plant residues and, in particular, on their C/N ratio. The growth of microbial colonies requires a fixed proportion of carbon and nitrogen so that their C/N ratio remains practically constant: thus, assuming the biomass C/N ratio is 8, for each part of nitrogen metabolized by microbes 24 parts of carbon are needed, of which 8 are metabolized and 16 are respired as CO₂ [6]. As a consequence, if the nitrogen content of the organic matter being decomposed is high (i.e., C/N < 24), mineralization proceeds unrestricted and mineral components in excess are released into the soil. On the contrary, when the litter is nitrogen poor (i.e., C/N > 24), microbes can use some of the mineral nitrogen, if any is available, through the process of immobilization. The modeling of this delicate balance is discussed in detail in Section 4.

Nitrate is easily soluble in water and, although this facilitates its uptake by plants, it also makes it prone to losses by leaching at high soil moisture levels. On the other hand, the positive charge of ammonium ions attracts them to the negatively charged surfaces of clays and humus, thus partially protecting them from leaching. Although held in an exchangeable form, this may be a problem for plant uptake, since the rate of release of the fixed ammonium is often too slow to fulfill plant needs. At high soil moisture levels (see Fig. 5), the process of denitrification may take place, releasing greenhouse nitrogen gases. Although important for environmental considerations, this problem is not essential to the soil–plant nitrogen balance and thus is not considered here.

Plant nitrogen requirements are met by two different mechanisms of root uptake: either passively through the soil solution during the transpiration process or actively by a diffusive flux driven by concentration gradients produced by the plant itself [9,17,40]. As this second mechanism is energy absorbing, the active uptake seems to take place only when the nitrogen demand by plants is higher than the passive supply by transpiration. If both mechanisms are insufficient to meet such a demand, the plants are subject to nitrogen deficit. On the other hand, if the concentration in the soil solution is high, the passive uptake may even overtake the actual plant demand. Plants appear to have little control on passive uptake and nitrogen excess may even result in toxicity [6].

3. Probabilistic modeling of soil moisture dynamics

The starting point of the model of soil moisture dynamics at the daily time scale is the stochastic differential equation for the soil water balance, vertically averaged over the active soil depth Z_r ,

$$nZ_r \frac{ds}{dt} = I(s, t) - E(s) - T(s) - L(s), \quad (1)$$

where n is the porosity, s is the relative soil moisture content, $I(s, t)$ is the rate of infiltration from rainfall, $E(s)$ and $T(s)$ are respectively the rates of evaporation and transpiration, and $L(s)$ is the rate of leakage or deep infiltration.

Following Rodriguez-Iturbe et al. [29], rainfall is represented as a Poisson process of storm arrivals in time with rate λ , each storm having a depth h , modeled as an exponentially distributed random variable with mean α . Rainfall results in an infiltration depth into the soil, $I(s, t)$, which is taken to be the minimum of h and $nZ_r(1 - s)$, to reflect the fact that only a fraction of h can infiltrate when the rainfall amount exceeds the storage capacity of the soil column. Excess rainfall produces runoff according to the saturation from below mechanism. Canopy interception can be included in the model as described by [29]. All the model results are interpreted at the daily time scale.

As opposed to the model by Rodriguez-Iturbe et al. [29] and Laio et al. [16], here it is important to distinguish between evaporation and transpiration, since the transpiration term is also used to model the plant nitrogen uptake. Evaporation from the soil is modeled as a linearly increasing function of soil moisture from 0 at the hygroscopic point, s_h , to E_w at the wilting point and then constant from there on. Transpiration, $T(s)$, is characterized by two different regimes: a stressed transpiration regime with a linear rise of $T(s)$ from 0 at s_w to T_{\max} at s^* , where s^* is the soil moisture level at which the plant begins to close stomata in response to water stress and T_{\max} is the maximum (i.e. under well-watered conditions) daily transpiration rate, which depends on climate and vegetation characteristics. In the unstressed regime, transpiration is decoupled from soil moisture and remains constant at T_{\max} . Thus $T(s)$ is represented as

$$T(s) = \begin{cases} 0 & 0 \leq s \leq s_w, \\ \frac{s - s_w}{s^* - s_w} T_{\max} & s_w < s \leq s^*, \\ T_{\max} & s^* < s \leq 1. \end{cases} \quad (2)$$

Assuming no interaction with the underlying soil layers and water table occurs, $L(s)$ represents vertical percolation with unit gradient

$$L(s) = \frac{K_s}{e^{\beta(1-s_{fc})} - 1} [e^{\beta(s-s_{fc})} - 1], \quad (3)$$

where K_s is the saturated hydraulic conductivity, s_{fc} is the field capacity, and $\beta = 2b + 4$ with b being the pore size distribution index [16].

The sum of the evapotranspiration and leakage losses $\chi(s) = E(s) + T(s) + L(s)$ is shown in Fig. 6. The values of s_h , s_w , s^* and s_{fc} are related to the corresponding soil matric potentials Ψ_{s,s_h} , Ψ_{s,s_w} , Ψ_{s,s^*} , and $\Psi_{s,s_{fc}}$ through empirically determined soil–water retention curves [16].

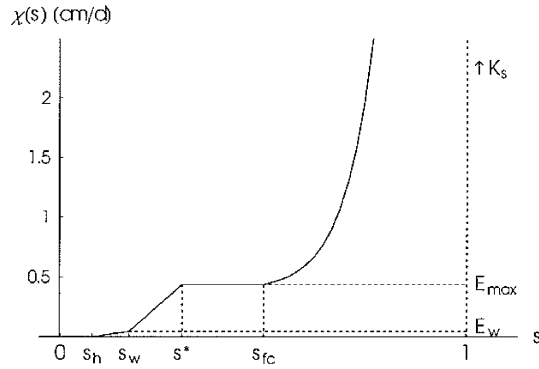


Fig. 6. Behavior of soil water losses (evapotranspiration and leakage), $\chi(s)$, as a function of the relative soil moisture for typical climate, soil, and vegetation characteristics in semiarid ecosystems ($E_{\max} = E_w + T_{\max}$).

As mentioned before, the active soil depth, Z_r , is assumed to be the same for both the water balance and carbon and nitrogen cycles. Its value is closely linked to the average rooting depth of plants [16] and it is considered to be constant in time. However, in a subsequent analysis changes in time of the root depth may be added to the model to express dynamical variations of Z_r as functions of plant and nutrient dynamics.

4. The carbon–nitrogen model

The highly intertwined carbon and nitrogen cycles are modeled employing five different pools, that represent the main components of the system (Fig. 7), that represent vertically averaged values of carbon and nitrogen concentrations over the active soil depth. The SOM is divided into three pools, that represent litter, humus, and microbial biomass, respectively, while the inorganic nitrogen in the soil is divided into ammonium (NH_4^+) and nitrate (NO_3^-). For the sake of model simplicity, no distinction is made of the different bacterial colonies and all of them are included in a single biomass pool; similarly, because of the high rate of nitrification, the presence of nitrite (NO_2^-) is usually very low and is neglected here. Our framework with three SOM pools is in agreement with the findings of Jenkinson [15] and Bolker et al. [5] who studied models with different numbers of compartments in the description of SOM and suggested using more than one and less than five pools for SOM. The use of a single pool for microbial biomass is justified by the scarce quantitative information available on soil microbial colonies.

Only the input of the added litter and the losses due to soil respiration, leaching, and plant uptake are considered of the external fluxes to the soil system, while other fluxes are neglected (that are less important at the daily-to-seasonal time scale), such as ammonium adsorption and desorption by clay colloids, volatilization,

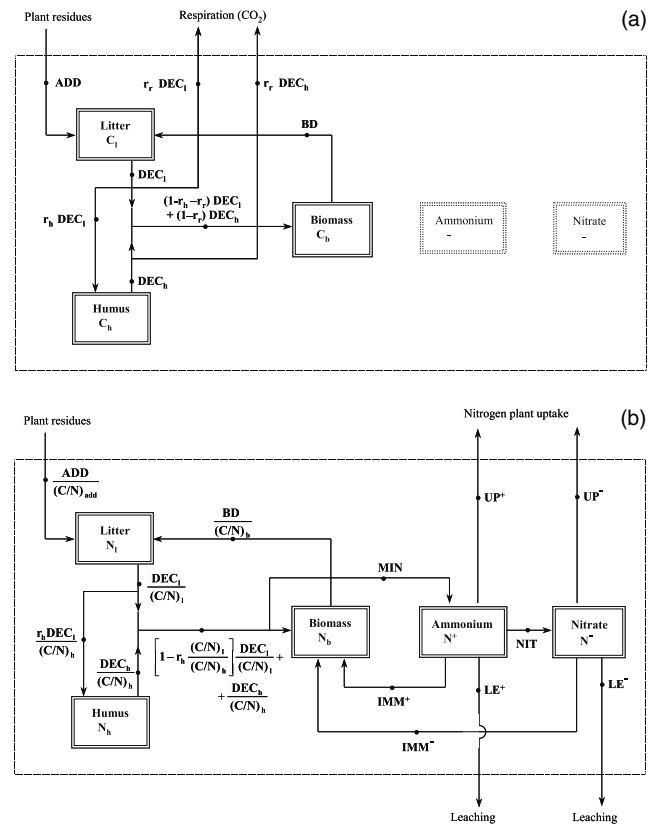


Fig. 7. Schematic representation of the main components of the model. (a) Soil carbon cycle and (b) soil nitrogen cycle. See text for details.

ammonium absorption, nitrogen input due to wet and dry deposition, biological fixation, and denitrification.

Since differences of some orders of magnitude are to be expected between the decomposition rate of the faster (proteins) and that of the slower (lignin) organic components [6], two or more pools of organic matter are often considered in the modeling scheme [6,12,13]. The separate consideration of litter and humus addresses this aspect since, in general, litter compounds have a faster decomposition rate than humic ones. Although a range of components is present in the SOM, the litter and humus pools are assumed to be characterized by unique values of the C/N ratio and of resistance to microbial decomposition, representing weighted averages of the various components.

The C/N ratios of the pools that contain organic matter are very important in the dynamics of the entire carbon and nitrogen cycles. Both the humus and the biomass C/N ratio remain approximately constant in time, while the litter C/N ratio may vary to some extent. The humus C/N ratio, $(C/N)_h$, is on the order of 10–12, that of biomass, $(C/N)_b$, is usually close to 8–12 (depending on the type of microbial community), while that of litter, $(C/N)_l$, ranges from 20 to over 50. As will

be seen, the constancy of $(C/N)_b$ and the variability of $(C/N)_l$ play an essential role in controlling the rates of decomposition, mineralization, and immobilization [6,13].

All the components of the soil carbon and nitrogen cycles considered in the present model are represented in Fig. 7. Eight state variables in terms of mass per unit volume of soil (e.g. grams of carbon or nitrogen per m^3 of soil) are needed to characterize the system, that is:

- C_l carbon concentration in the litter pool;
- C_h carbon concentration in the humus pool;
- C_b carbon concentration in the biomass pool;
- N_l organic nitrogen concentration in the litter pool;
- N_h organic nitrogen concentration in the humus pool;
- N_b organic nitrogen concentration in the biomass pool;
- N^+ ammonium concentration in the soil;
- N^- nitrate concentration in the soil.

The temporal dynamics of such variables are controlled by a system of as many coupled differential equations that describe the balance of carbon and nitrogen in the various pools. All the equations represent balances of fluxes of nitrogen or carbon in terms of mass per unit volume per unit time (e.g., $gm^{-3}d^{-1}$). Since many of the fluxes are greatly dependent on soil moisture content, the system is coupled to the soil moisture evolution, Eq. (1). In this way, the main hydrologic control on the carbon and nitrogen cycles is explicitly considered.

4.1. The litter pool

According to the fluxes depicted in Fig. 7, the carbon balance equation for the litter pool can be written as

$$\frac{dC_l}{dt} = ADD + BD - DEC_l. \quad (4)$$

The term ADD is the external input in the system, representing the rate at which carbon in plant residues is added to the soil and made available to the attack of the microbial colonies. The rate and composition of added litter may change in time due to variations in vegetation biomass. In the case discussed by D'Odorico et al. [8], ADD and its C/N ratio are assumed to be constant in time; however, the input parameter ADD should be expressed as a function of time as well as of vegetation dynamics when either the effect of litterfall seasonality or the occurrence of exceptional events (e.g., fires, hurricanes etc.) may lead to important temporal variations of the added litter.

The term BD represents the rate at which carbon returns to the litter pool due to the death of microbial biomass. We simply use a linear dependence on the

amount of microbial biomass, i.e. $BD = k_d C_b$, without explicitly considering the influence of environmental factors, such as temperature and soil moisture.

Finally, the term DEC_l represents the carbon output due to microbial decomposition. It is modeled using first order kinetics [4,11,13]

$$DEC_l = [\varphi f_d(s) k_1 C_b] C_l, \quad (5)$$

where the first order rate term in square brackets is rather complicated, due to its dependence on many different factors. The coefficient φ is a nondimensional factor that accounts for a possible reduction of the decomposition rate when the litter is very poor in nitrogen and the immobilization is not sufficient to integrate the nitrogen required by the bacteria. We will return later to this point. $f_d(s)$ is another nondimensional factor, that describes soil moisture effects on decomposition. Following Cabon et al. [7] and Gusman and Marino [11], we model the soil moisture control on aerobic microbial activity and decomposition via a linear increase up to field capacity and a hyperbolic decrease up to soil saturation

$$f_d(s) = \begin{cases} \frac{s}{s_{fc}} & s \leq s_{fc}, \\ \frac{s_{fc}}{s} & s > s_{fc}. \end{cases} \quad (6)$$

As shown in Fig. 8, Eq. (6) satisfactorily expresses the qualitative behavior discussed in the Introduction (Fig. 5). The value of the constant k_1 defines the rate of decomposition for the litter pool as a weighted average of the decomposition rates of the different organic compounds in the plant residues. Its average value is usually much higher than the corresponding value for humus. The rate of decomposition also depends on the microbial biomass concentration, C_b [13], whose evolution is described later. The relationship between the concentration of microbial biomass and its activity is assumed to be linear.

The nitrogen balance in the litter pool is similar to Eq. (4), with each term divided by the C/N ratio of its respective pool, i.e.

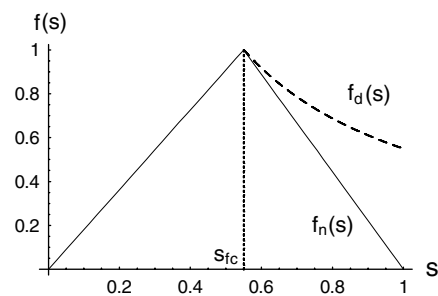


Fig. 8. Fundamental dependence of decomposition and nitrification on the relative soil moisture.

$$\frac{dN_l}{dt} = \frac{ADD}{(C/N)_{add}} + \frac{BD}{(C/N)_b} - \frac{DEC_l}{(C/N)_l}. \quad (7)$$

$(C/N)_{add}$, the C/N ratio of the added plant residues, ranges from 10/1 in legumes and young green leaves to more than 200/1 in sawdust [6]. This large variability may produce pronounced changes in the C/N ratio of the litter pool, which has a very important role in regulating decomposition, immobilization, and mineralization.

4.2. The humus pool

The balance equation for carbon in the humus pool is

$$\frac{dC_h}{dt} = r_h DEC_l - DEC_h, \quad (8)$$

where the only input is represented by the fraction r_h of the decomposed litter that undergoes humification (see Fig. 7). The coefficient r_h , which is sometimes referred to as the “isohumic coefficient” [40], is in the range 0.15–0.35 [6], depending on the composition of plant residues.

The output due to humus decomposition is modeled in the same way as litter decomposition,

$$DEC_h = [\varphi f_d(s) k_h C_b] C_h, \quad (9)$$

where the value of the constant k_h , which encompasses the various components of the humus pool (see Fig. 3), is much smaller than the corresponding value for the litter pool, because of the greater resistance of the humic substances to the microbial attack.

The nitrogen balance equation may be simply obtained by dividing Eq. (8) by $(C/N)_h$, i.e.

$$\frac{dN_h}{dt} = r_h \frac{DEC_l}{(C/N)_h} - \frac{DEC_h}{(C/N)_h}, \quad (10)$$

This implies the assumption that the products of the humification process from litter have the same characteristics, and thus also the same C/N ratio, as the soil humus. As a consequence, the value of $(C/N)_h$ remains constant in time, making Eq. (10) redundant. The fraction r_h cannot exceed $(C/N)_h/(C/N)_l$, as is clear from the condition that the fraction of nitrogen that enters the humus pool from the litter decomposition cannot exceed the total nitrogen flux from the litter decomposition, i.e.

$$r_h \frac{DEC_l}{(C/N)_h} \leq \frac{DEC_l}{(C/N)_l}.$$

4.3. The microbial biomass pool

The carbon balance in the biomass pool is given by

$$\frac{dC_b}{dt} = (1 - r_h - r_r) DEC_l + (1 - r_r) DEC_h - BD. \quad (11)$$

The input is represented by the fraction of organic matter that is incorporated by the microorganisms from

litter and humus decomposition (see Fig. 7). The constant r_r ($0 \leq r_r \leq 1 - r_h$) defines the fraction of decomposed organic carbon that goes into respiration (CO_2 production), which is usually estimated in the 0.6–0.8 interval [6]. The only output is BD, which has already been defined when discussing Eq. (4).

The balance of the nitrogen component in the biomass may be expressed as

$$\begin{aligned} \frac{dN_b}{dt} = & \left[1 - r_h \frac{(C/N)_l}{(C/N)_h} \right] \frac{DEC_l}{(C/N)_l} + \frac{DEC_h}{(C/N)_h} \\ & - \frac{BD}{(C/N)_b} - \Phi. \end{aligned} \quad (12)$$

The first two terms on the r.h.s. represent the incoming nitrogen from decomposition and do not contain r_r because the respiration process only involves the carbon component. The coefficient in brackets preceding the first term on the r.h.s. accounts for the nitrogen fraction that goes into the humified litter. As already mentioned regarding the first term on the r.h.s. of Eq. (10), the fraction $(C/N)_l/(C/N)_h$ is usually greater than one, because the humified litter is richer in nitrogen than the litter itself. The third term of Eq. (12) is the output of nitrogen due to microbial death, while the fourth term, Φ , takes into account the contribution due to either the net mineralization or to the immobilization. This term is now discussed in detail, since it is relevant to the entire dynamics and synthesizes the governing role of the SOM carbon-to-nitrogen ratio.

4.4. Mineralization and immobilization rates

The term Φ in Eq. (12) attains positive or negative values in relation to the difference between the rate of gross mineralization and the total rate of immobilization of NH_4^+ , IMM^+ , and NO_3^- , IMM^- , i.e.

$$\Phi = MIN - IMM, \quad (13)$$

where

$$IMM = IMM^+ + IMM^-. \quad (14)$$

Since it is the net flux between the various pools that is important to the nitrogen balance, only the net mineralization and immobilization amounts need to be modeled. This can be done as if they were mutually exclusive processes. Thus, when $\Phi > 0$, we assume that

$$\begin{cases} MIN = \Phi, \\ IMM = 0, \end{cases} \quad (15)$$

while, when $\Phi < 0$,

$$\begin{cases} MIN = 0, \\ IMM = -\Phi. \end{cases} \quad (16)$$

The switch between the two states is determined by the condition that $(C/N)_b$ is constant in time. Accordingly, when the average C/N ratio of the biomass is

lower than the value required by the microbial biomass, the decomposition results in a surplus of nitrogen, which is not incorporated by the bacteria, and net mineralization takes place. If, instead, the decomposing organic matter is nitrogen poor, bacteria try to meet their nitrogen requirement by increasing the immobilization rate from ammonium and nitrate, thus impoverishing the mineral nitrogen pools. In the case where the nitrogen supply from immobilization is not enough to ensure a constant C/N ratio for the biomass, the rates of decompositions are reduced to below their potential values by means of the parameter φ (e.g., see Eqs. (5) and (9)) as follows.

The condition of constant C/N ratio for the biomass pool is implemented analytically as

$$\frac{d(C/N)_b}{dt} = \frac{dC_b}{dt} - \frac{dN_b}{dt} (C/N)_b = 0, \quad (17)$$

which, using (11) and (12), yields

$$\begin{aligned} \Phi &= \text{DEC}_h \left[\frac{1}{(C/N)_h} - \frac{1-r_r}{(C/N)_b} \right] + \text{DEC}_l \left[\frac{1}{(C/N)_l} \right. \\ &\quad \left. - \frac{r_h}{(C/N)_h} - \frac{1-r_h-r_r}{(C/N)_b} \right] \\ &= \varphi f_d(s) C_b \left\{ k_h C_h \left[\frac{1}{(C/N)_h} - \frac{1-r_r}{(C/N)_b} \right] \right. \\ &\quad \left. + k_l C_l \left[\frac{1}{(C/N)_l} - \frac{r_h}{(C/N)_h} - \frac{1-r_h-r_r}{(C/N)_b} \right] \right\}, \end{aligned} \quad (18)$$

Notice that Eq. (18), and not (12), is the real dynamical equation to be associated to Eq. (11) for the biomass evolution. The previous condition makes Eq. (12) redundant, as the biomass C/N ratio is set constant.

When the term in curly brackets of Eq. (18) is positive, net mineralization takes place, while no net immobilization occurs, as indicated by Eq. (15). In such conditions, humus and litter decomposition proceeds unrestricted and the parameter φ is equal to 1.

In the opposite case, when the term in curly brackets of Eq. (18) is negative, net mineralization is halted and immobilization sets in Eq. (16). The latter is partitioned proportionally between ammonium and nitrate on the basis of their concentrations and according to two suitable coefficients, k_i^+ and k_i^- , i.e.

$$\begin{cases} \text{IMM}^+ &= \frac{k_i^+ N^+}{k_i^+ N^+ + k_i^- N^-} \text{IMM}, \\ \text{IMM}^- &= \frac{k_i^- N^-}{k_i^+ N^+ + k_i^- N^-} \text{IMM}. \end{cases} \quad (19)$$

The rate of immobilization may be limited by environmental factors, biomass concentration, and—especially—by insufficient mineral nitrogen. For this reason, we assume the existence of an upper bound for the rate of mineralization, i.e.

$$\text{IMM} \leq \text{IMM}_{\max} \quad (20)$$

which after Eq. (18) becomes

$$\begin{aligned} -\varphi f_d(s) C_b \left\{ k_h C_h \left[\frac{1}{(C/N)_h} - \frac{1-r_r}{(C/N)_b} \right] \right. \\ \left. + k_l C_l \left[\frac{1}{(C/N)_l} - \frac{r_h}{(C/N)_h} - \frac{1-r_h-r_r}{(C/N)_b} \right] \right\} \leq \text{IMM}_{\max}. \end{aligned} \quad (21)$$

Since immobilization is the conversion of inorganic nitrogen ions into organic form operated by microorganisms which incorporate mineral ions to synthesize cellular components [4, p. 405], it is assumed that it depends on the concentration of the microbial biomass and soil moisture in a similar way to the decomposition process,

$$\text{IMM}_{\max} = (k_i^+ N^+ + k_i^- N^-) f_d(s) C_b. \quad (22)$$

Two possible regimes thus exist for immobilization. In the first one, immobilization is unrestricted: the immobilization rate is lower than IMM_{\max} , and the coefficient φ is equal to 1. This means that the bacteria can meet their nitrogen requirement and decompose the organic matter at a potential rate. The second regime occurs when the requirement of mineral nitrogen to be immobilized becomes higher than the maximum possible rate and the mineralization rate is reduced. This is accomplished in the model by reducing φ to a value lower than 1, so that the immobilization rate is equal to IMM_{\max} . By imposing the equality in Eq. (21), i.e. $\text{IMM} = \text{IMM}_{\max}$, the value of φ by which the decomposition rates must be reduced (Eqs. (5) and (9), respectively) is obtained,

$$\begin{aligned} \varphi &= -(k_i^+ N^+ + k_i^- N^-) / \left(k_h C_h \left[\frac{1}{(C/N)_h} - \frac{1-r_r}{(C/N)_b} \right] \right. \\ &\quad \left. + k_l C_l \left[\frac{1}{(C/N)_l} - \frac{r_h}{(C/N)_h} - \frac{1-r_h-r_r}{(C/N)_b} \right] \right). \end{aligned} \quad (23)$$

Eqs. (18) and (23) regulate the entire dynamics of decomposition, mineralization, and immobilization. Their functioning is illustrated by the numerical examples in Fig. 9. In the first example (upper rows of numbers in the figure) the litter C/N ratio is rather low (20) so that the decomposed organic matter from litter and humus (node A in Fig. 9) is nitrogen rich, i.e. with an overall C/N ratio lower than 8, which is the assumed C/N ratio of the microbial biomass. As a consequence, a fraction of nitrogen must go into net mineralization ($\Phi > 0$) and the inequality in (21) is satisfied with $\varphi = 1$. In the second example $(C/N)_l = 30$, therefore the (C/N) ratio in A is higher than 8. Immobilization of some mineral nitrogen is thus necessary to maintain a C/N ratio equal to 8. The rate of net immobilization is determined by Eq. (18). The inequality in (21) is satisfied as the resulting immobilization rate is lower than the maximum potential one ($\text{IMM}_{\max} = 1$), and φ is equal to 1. The third

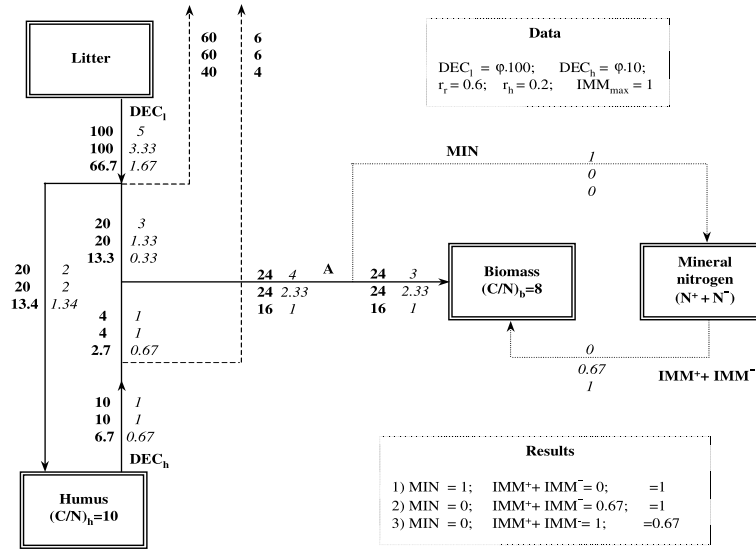


Fig. 9. Numerical examples of decomposition, mineralization, and immobilization rates. The three examples have the features reported in the upper right corner of the figure in common, while they differ in the value of the carbon-to-nitrogen ratio of the litter pool, which is equal to 20 in the first example (upper rows of numbers), equal to 30 in the second (central rows), and equal to 40 in the third (lower rows). The boldface numbers refer to carbon fluxes, the italic numbers to nitrogen fluxes. The resulting mineralization and immobilization rates, along with the corresponding values of ϕ , are reported in the lower right corner of the figure.

case presents an example of nitrogen-poor litter, $(C/N)_l = 40$, where the required net immobilization rate (equal to 1.5) is greater than $IMM_{max} = 1$. This means that the inequality in (21) is not satisfied and the decomposition rate must be reduced by imposing $\phi = (1/1.5) = 0.67$, as obtained from (23). With this value of ϕ , the C/N ratio of the fluxes in the biomass pool is equal to 8, and the immobilization rate is equal to IMM_{max} .

4.5. The mineral nitrogen in the soil

The balance of ammonium and nitrate in the soil can be modeled respectively as

$$\frac{dN^+}{dt} = MIN - IMM^+ - NIT - LE^+ - UP^+, \quad (24)$$

and

$$\frac{dN^-}{dt} = NIT - IMM^- - LE^- - UP^-, \quad (25)$$

in which the mineralization and immobilization rates have already been described. The nitrification rate can be modeled as first order kinetics, i.e.

$$NIT = f_n(s)k_n C_b N^+, \quad (26)$$

where C_b expresses the dependence of nitrification on microbial activity. The constant k_n defines the rate of nitrification, while $f_n(s)$ (nondimensional) accounts for the soil moisture effects on nitrification. As seen in Fig. 5, the optimum conditions for nitrification are very similar to those for decomposition, with the difference that nitrification tends to zero at soil saturation [18,36].

We model this behavior with a linear increase up to field capacity followed by a linear decrease to soil saturation (see Fig. 8),

$$f_n(s) = \begin{cases} \frac{s}{s_{fc}} & s \leq s_{fc}, \\ \frac{1-s}{1-s_{fc}} & s > s_{fc}. \end{cases} \quad (27)$$

For both ammonia and nitrate, leaching occurs when the nitrogen in the soil solution percolates below the root zone. It is thus simply proportional to the leakage term $L(s)$ modeled in Eq. (3),

$$LE^\pm = a^\pm \frac{L(s)}{snZ_r} N^\pm, \quad (28)$$

where $L(s)$ is divided by the volume of water per unit area, snZ_r , so that the term $(L(s)/snZ_r)$ assumes the dimension of the inverse of time. The nondimensional coefficients a^\pm , $0 \leq a^\pm \leq 1$, are the fractions of the dissolved ammonium and nitrate, respectively, and are related to the corresponding solubility coefficients. Since nitrate is a mobile ion, a^- can be taken to be equal to one, while a^+ is much lower, as a large fraction of ammonium is absorbed by the soil matrix. This is why leaching of ammonium is seldom important. At very low soil moisture levels, when liquid water becomes a highly disconnected system, the coefficients a^\pm may be reduced by evaporation and become soil moisture dependent, $a^\pm = a^\pm(s)$. Although this is certainly not important for leaching, it may modify the water uptake at low soil moisture levels, as discussed in the following section.

The last terms of Eqs. (24) and (25), UP^+ and UP^- , are the ammonium and nitrate plant uptake rates. Their

modeling, which is crucial for the simulation of nitrogen dynamics in natural ecosystems, is now described in detail.

4.6. Nitrogen uptake by plants

The process of nitrogen uptake by plants is complex and not yet completely understood. For this reason, its simplified modeling is rather delicate and requires a detailed justification. As many aspects of nitrogen uptake are similar for nitrate and ammonium, we will discuss them together, pointing out the differences when necessary.

For both ammonium and nitrate, passive and active uptake can be regarded as additive processes [40], i.e.

$$UP^{\pm} = UP_p^{\pm} + UP_a^{\pm}. \quad (29)$$

The passive uptake can simply be modeled as proportional to the transpiration rate, $T(s)$, that is modeled in Eq. (2), and to the nitrogen concentration in the soil solution, i.e.

$$UP_p^{\pm} = a^{\pm} \frac{T(s)}{snZ_r} N^{\pm}, \quad (30)$$

where, in a similar way to leaching, $T(s)$ must be divided by snZ_r for dimensional reasons and a^{\pm} represent the fraction of dissolved inorganic nitrogen. As previously stated, a^{\pm} may be reduced at very low soil moisture levels, $a^{\pm} = a^{\pm}(s)$, but very little information seems to be available to this regard, although it may be important for the modeling of passive uptake under very dry conditions. Given the behavior of the transpiration rate defined in Eq. (2), the passive uptake has the form shown in light gray in Fig. 10. The reason for the decrease above s^* is the dilution of the soil solution.

The active uptake mechanism is closely associated with the plant metabolic processes [9,17,40]. It is accomplished by establishing a concentration gradient between the root surface and the soil, which triggers a diffusion flux of the nitrogen ions. The intensity of the flux is limited by the gradient itself which is controlled in part by the plant on account of its nitrogen demand and rate of passive uptake and by the diffusion coefficient. Accordingly, we assume that the plant tries to compensate for the deficit with the active mechanism of uptake only if the passive uptake is lower than a given plant demand, DEM^{\pm} (e.g., $g d^{-1} m^{-3}$ of soil). When the diffusion of nitrogen ions in the soil is limiting, the active uptake is assumed to be proportional to the nitrogen concentration in the soil through a suitable diffusion coefficient, otherwise active uptake is simply the difference between the demand and the passive component (i.e. the total uptake satisfies the plant demand). Three possible cases thus occur in the representation of the active component,

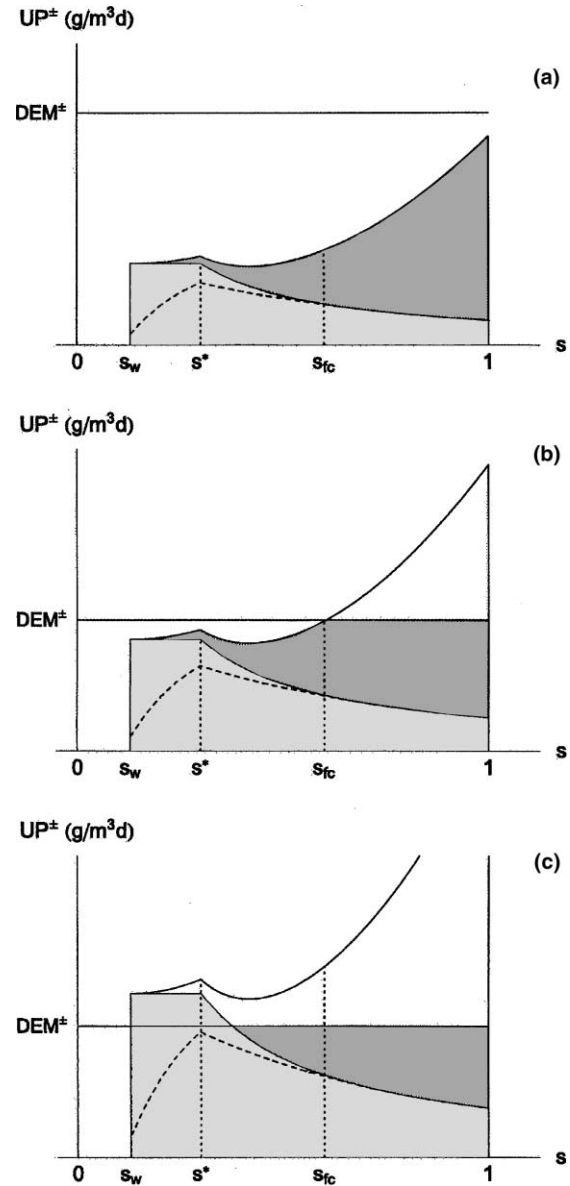


Fig. 10. Plant nitrogen uptake versus soil moisture for decreasing concentrations of mineral nitrogen from (a) to (c). The horizontal line represents the plant demand, while the other continuous lines define the potential active and passive uptakes. As the actual uptake is limited by plant demand, the light gray regions represent the actual passive component of the uptake and the dark gray regions the actual active component. The dashed lines refer to the possible nonlinear reduction of the solubility coefficients with soil moisture, $a^{\pm}(s)$, which lowers the passive uptake.

$$UP_a^{\pm} = \begin{cases} 0 & \text{if } DEM^{\pm} - UP_p^{\pm} < 0, \\ k_u N^{\pm} & \text{if } k_u N^{\pm} < DEM^{\pm} - UP_p^{\pm}, \\ DEM^{\pm} - UP_p^{\pm} & \text{if } k_u N^{\pm} > DEM^{\pm} - UP_p^{\pm} > 0. \end{cases} \quad (31)$$

The term $k_u N^{\pm}$ expresses the dependence of the diffusive flux on the concentration gradient between the root surface and the bulk of the soil, which in first

approximation is taken to be proportional to the nitrogen concentration in the solution (i.e. the concentration within the roots is considered to be nearly zero). The parameter k_u (d^{-1}) describes the dependence of the diffusion process on the soil moisture level and can be modeled as

$$k_u = \frac{a^\pm}{snZ_r} F s^d, \quad (32)$$

where the term (a^\pm/snZ_r) transforms the concentration in the soil into a concentration in solution, the term F is a rescaled diffusion coefficient [40], and d expresses the nonlinear dependence of the diffusion process on soil moisture. If one considers that the diffusion coefficient is often related to the product between soil moisture and a tortuosity factor (which in turn has a quadratic dependence on soil moisture), a typical value of d is around 3. No attempt is made to relate the coefficient F to the real diffusion coefficients for ammonium and nitrate, and F is merely chosen in such a way that the active contribution to nitrogen uptake is in the 50–80% range of the total uptake at high values of soil moisture ([9] and references therein), as shown in Fig. 10.

When the nitrogen concentration is low compared to the plant demand (Fig. 10a), the active uptake is limited by diffusion and plants are subject to nitrogen deficit; on the other hand, when the nitrogen concentration is high (Fig. 10c), plant requirements are usually met, either by passive uptake alone at low soil moisture values (i.e. when the nitrogen in the solution is more concentrated) or by both active and passive uptake at higher soil moisture values. As already noticed, the passive uptake may overtake the plant demand and, if this situation lasts for some time, the excessive nitrogen uptake may have harmful effects and decrease the plant growth rate [40]. At low soil moisture levels the role of the “solubility coefficient” a^\pm may also become important: in the case of a nonlinear dependence on soil moisture, a reduction in the passive uptake at low soil moisture levels appears (dashed line in Figs. 10a–c).

Although the demand must be a well defined value in our mechanistic model, it is clear that in reality DEM is an average value that is representative of typical nitrogen requirements of a given species. Since it is much more difficult to distinguish between ammonium and nitrate, we will consider an overall nitrogen demand and then, according to the type of plant, we will split it proportionally into DEM^+ and DEM^- . Possible indications for the total nitrogen demand can be obtained by analyzing the soil–plant system. When an ecosystem has reached stable conditions, on annual time scales, the amount of uptaken nitrogen tends to balance that returned to the soil in the form of plant litter [17,40]. It is thus reasonable to assume that plant nitrogen demand is of the same order of magnitude (or a little bit higher) as the average rate of nitrogen added with the litter. Such a

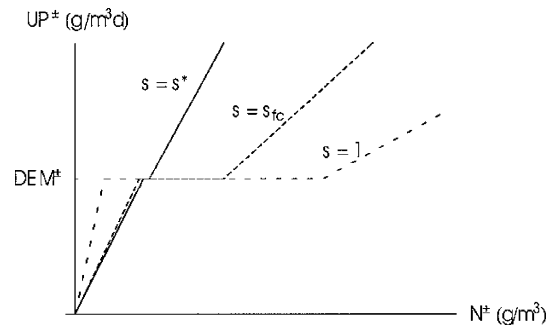


Fig. 11. Nitrogen plant uptake as a function of nitrogen concentrations for constant values of soil moisture.

linkage confers an essential regulative control to both the rate of added litter and the plant nitrogen demand on the rate of nitrogen recycling in the ecosystem. Physiological characteristics of plants and environmental conditions play an important role in this aspect.

The present nitrogen uptake model is in part a demand driven one [13], whose behavior is in good agreement with the results reported in literature. It is usually accepted that the dependence of nitrogen uptake on nitrogen concentration is described by Michaelis–Menten kinetics, corrected with a linear increase at high nitrogen concentrations [9,14]. Such a behavior corresponds to an increasing rate of uptake up to a saturation concentration followed by a further increase at very high nitrogen concentrations. Fig. 11 shows the total nitrogen uptake in our model as a function of the nitrogen concentration. It is clear that, for relatively high soil moisture values, the behavior is similar to that just discussed. The plateau where the uptake remains constant is found at DEM and its width depends on the soil moisture value. The following linear increase at high N concentrations, due to the passive uptake, presents a lower slope than the first part. Lower soil moisture values give a similar behavior, but with a narrower plateau.

4.7. Summary of the model

The evolution of carbon and nitrogen in the soil is described by Eqs. (4), (7), (8), (11), (24), and (25), along with conditions (15), (16), and (21) that define the net mineralization and immobilization. The system is coupled with the soil moisture evolution equation (1), which accounts for the hydrologic forcing.

By summing the three equations for the carbon and the five for the nitrogen, one obtains the corresponding differential equations for the total carbon and nitrogen in the system, $C_{tot} = C_l + C_h + C_b$ and $N_{tot} = N_l + N_h + N_b + N^+ + N^-$, respectively. In particular, from the sum of Eqs. (4), (8), and (11) one obtains

$$\frac{dC_{\text{tot}}}{dt} = \text{ADD} - r_i \text{DEC}_i - r_h \text{DEC}_h \quad (33)$$

and from the sum of Eqs. (7), (10), (12), (24), and (25)

$$\frac{dN_{\text{tot}}}{dt} = \frac{\text{ADD}}{(C/N)_{\text{add}}} - \text{LE}^+ - \text{UP}^+ - \text{LE}^- - \text{UP}^-. \quad (34)$$

The terms in Eqs. (33) and (34) represent the global gains and losses of the soil system. In this way the continuity of nitrogen and carbon in the soil system is ensured, closely following the scheme of Fig. 7. In some aspects the structure of the present model is similar to that considered by Birkinshaw and Ewen [4]. In their paper, however, the reduction in the decomposition due to insufficient immobilization was not taken into account and, as a consequence, the closure of the carbon and nitrogen balance was not complete.

5. Final comments

The model presented in this paper addresses the role of hydrological processes on the soil carbon and nitrogen cycles from the mathematical modeling point of view. The resulting scheme is a system of eight nonlinear ordinary differential equations for the carbon and nitrogen dynamics in the soil, driven by a nonlinear stochastic differential equation that describes the water balance at a point. The influence of rainfall, vegetation, and soil characteristics is directly incorporated, through soil moisture dynamics, into the process of mineralization and immobilization, plant nitrogen uptake, and leaching.

In a companion paper by D'Odorico et al. [8], the model is applied to the savanna ecosystem of Nylsvley in South Africa in order to investigate the role of its most important parameters and the impact of different climate, soil, and vegetation characteristics, through the resulting soil moisture dynamics, on the soil carbon and nitrogen cycles. The aim is to understand how the temporal soil moisture fluctuations are dynamically transmitted through the various pools of the system and obtain a quantitative probabilistic description.

Future research will include the effect of soil temperature as well as the closure of the soil–plant nitrogen cycle through the coupling with plant-growth models. Possible simplifications of the model will be also studied, indicating conditions under which more tractable frameworks can be used.

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