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Modelling the competition for nitrogen between plants and microflora as a function of soil heterogeneity

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Abstract

Plant–microbe competition for inorganic N is a common phenomenon in soils, and the traditional view is that microorganisms are much stronger competitors than are plant roots. We challenged this view, hypothesizing that the balance between the two competitors is strongly dependent on the spatial heterogeneity of the soil. We constructed a model to explore this hypothesis. The model was structured to simulate a laboratory experiment where N-limited plants were grown in a soil containing two types of microbial "hotspots"; with high potential for either net N-immobilization (straw particles) or net N mineralization (clover particles). In this experiment (Wang and Bakken, 1997), plant roots appeared to compete successfully with microorganisms for inorganic N, and their competitiveness depended strongly on the distance (3, 6, 9 or 12 mm) between the layers of straw and clover material. Most model parameters were taken from the literature, whilst some parameters were estimated by least square model optimization using selected treatments within the experiment. The parameterized model was then statistically evaluated against treatments not used in the parameterization. The model efficiently simulated the observed transient inorganic N accumulation in unplanted soil and its dependency on distance between hotspots (modelling efficiency, EF = 0.611). It also captured very well the plant N uptake and its dependency of the distance between hotspots (EF = 0.860). The modelling exercise underscored the importance of soil heterogeneity in determining the outcome of the competition between plant roots and microorganisms for inorganic N in soil. Spatial segregation of hotspots with net N-immobilization and net N mineralization is likely to be the rule rather than the exception in natural soils. This has a profound impact on the N dynamics of soil plant systems, and it should be taken into account for the interpretation of experiments (such as ^{15}N pool dilution experiments) as well as in general models for the C and N dynamics of soil–plant systems.

Keywords: Competition; Hotspots; Microorganisms; Model; Nitrogen; Plant roots

1. Introduction

Soil microorganisms potentially compete with plant roots for N when their available organic substrate has low nitrogen content (Kaye and Hart, 1997; Schimel et al., 1989). This microbial competition for mineral N could be enhanced by the release of soluble carbon substrates from growing roots, unless other factors limit microbial activity (Cheng et al., 1996). Such inter-kingdom competition for nitrogen appears to be the rule rather than the exception (Jackson et al., 1989), with potential implications both for plant productivity and for microbial carbon and nitrogen transformations.

Plant roots appear to be able to assimilate organic N, either directly (Chapin et al., 1993) or indirectly via their mycorrhizal symbiont (Johansen et al., 1992; Read, 1991). Such mechanisms may hypothetically strengthen the competitive ability of plants vis a vis microorganisms, since they allow plants direct access to the pools of organic N. Quantitative assessments of such direct organic N uptake by plant roots and symbionts suggest, however, that inorganic N uptake represents the major route of N uptake by most plants (Kaye and Hart, 1997).

For various reasons, microorganisms have been assumed to be much stronger competitors for inorganic N than plant roots (see review by Kaye and Hart, 1997). Wang and Bakken (1997) obtained, however, indirect evidence that plant roots may compete successfully for inorganic N by "interception": In constructed soil microcosms, they regulated the distance between "hotspots" of microbial net N mineralization (clover litter) and microbial net N assimilation (straw). In microcosms without plants, the N

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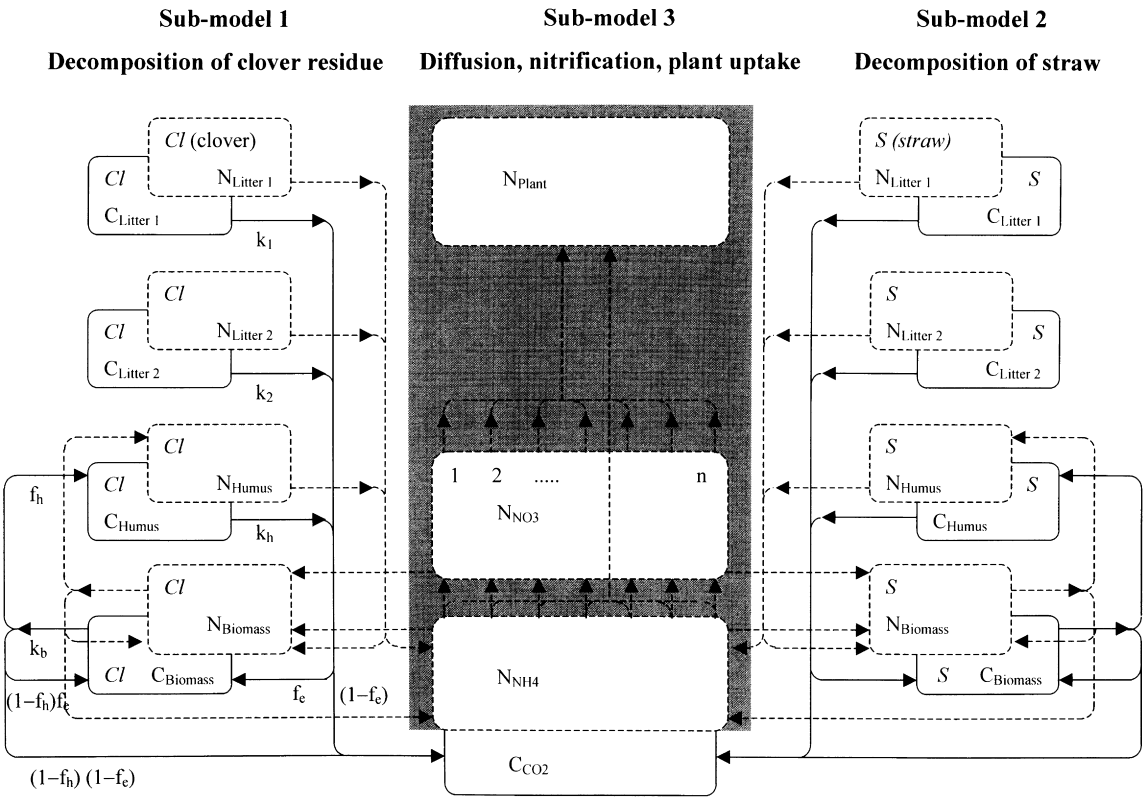

Fig. 1. Flow chart of the model. Solid lines denote carbon and dotted lines nitrogen state variables (rectangles) and flows (arrows). Submodels 1 and 2 govern the decomposition of clover residues and straw, respectively, and submodel 3 governs nitrification, plant N uptake and diffusion of ammonium-N and nitrate-N.

mineralized in clover litter hotspots was quickly assimilated by the microorganisms decomposing the straw. In microcosms with plants, a large share of the N mineralized in clover litter hotspots was captured by the plants, and this share was strongly controlled by the distance (0, 3, 6, 9 and 12 mm) between clover litter and straw. The results strongly suggest a direct competition for inorganic N between plant roots and microorganisms, depending on the spatial distribution of substrates in the soil. Hence, root uptake of organic N (direct or via mycorrhiza) is not a necessary prerequisite for plant roots to successfully compete with microorganisms for N.

In the present model study, we elucidate this spatio-temporal dependency of the inorganic N competition between plant roots and soil microorganisms by modelling the results obtained by Wang and Bakken (1997). We used a simple diffusion model coupled to traditional C- and N-simulations of the microbial processes within the different hotspots. Adequate simulations of the events in the two types of hotspots were obtained by parameterization using independent datasets. The model efficiently simulated the dependency of microbial and plant assimilation of N on the distance between the hotspots, thus demonstrating that diffusion limitations may sufficiently explain the result of the competition. The results underline the necessity to study spatio-temporal variations in net N transformations (at scales of mm and days) in order to understand and predict the dynamics of microbial C and N transformations in the soil and their interaction with plant roots.

2. Materials and methods

2.1. Experimental

Model construction, calibration and testing was based on different sections of the competition experiments by Wang and Bakken (1997), which will be described in some detail. The experiments were designed for exploring how plant-microbe competition would be affected by the spatial distribution of hotspots with net N mineralization (clover residues, C:N ratio = 17.5) and net N immobilization (barley straw, C:N ratio = 81.9) in the soil. The clover and straw was finely ground and placed as discrete, vertical layers separated by soil, which was a silty subsoil with low content of organic material (0.15 mg organic N and 2.15 mg organic C per g). A series of different microcosms was constructed, all containing the same amount of materials (2.5 g clover, 5.0 g straw and 200 g soil), but with different thicknesses of the soil layers separating straw and clover (3, 6, 9, and 12 mm). In addition, one series of pots was prepared by thoroughly mixing soil and residues (= MIX). The

variation of the thickness of the soil layers separating clover and straw was achieved by varying the numbers of layers per pot. This resulted in different thicknesses of the clover and straw layers as well. The thickness of the residue layers in pots with 3, 6, 9 and 12 mm thick soil layers was 0.9, 1.7, 2.4 and 3.0 mm for straw and 0.6, 1.1, 1.6 and 2.0 mm for clover, respectively.

One-week-old barley (*Hordeum vulgare* L.) plants were transplanted into one half of the pots (three plants per pot), the rest were kept unplanted. There were thus five planted treatments (PMIX, P3, P6, P9, P12) and five unplanted treatments (UMIX, U3, U6, U9, U12). The pots were incubated at room temperature for 42 days. Both planted and unplanted pots were watered daily with distilled water up to target weight (22 ml cm^{-3}, equivalent to 50% air filled porosity) and partly covered with aluminium foil to reduce evaporation. In order to minimize vertical water movement, water was sprayed gently onto the soil surface. On each of days 14, 21, 28, 35 and 42, one pot per treatment was sampled destructively. Concentrations of soil inorganic N, total N in barley plants and residual organic N in clover residues and straw were determined on these occasions.

2.2. Model description

The model comprises three integrated submodels. The clover and straw decomposition is simulated by submodels 1 and 2 (identical models, but with different initial sizes of C and N pools). Submodel 3 simulates the diffusion transport of mineral N in the soil layer, plant uptake of mineral N, and oxidation of ammonium to nitrate. In the real pots, there were many parallel layers (repeated layers of soil separating repeated layers of clover and straw), but the simulations were done as if there was just one layer of soil separating one layer of clover material and one layer of straw. Gaseous losses are not considered. The model flow chart is shown in Fig. 1 and all state variables and parameters are described in the Appendix A.

For simulation of the coupled microbial C and N transformations during clover- and straw decomposition we used the model SOILN_NO (Vold et al., 1999). This model was reprogrammed in MATLAB 5.3 (Release 11, The MathWorks, Inc., 1999, Natick MA, US) and duplicated to enable parallel simulation of the processes in the clover and straw layers (different size of the C- and N-pools). Nitrification was not included since this process was handled by submodel 3. In brief, SOILN_NO is a modified version of the SOILN model (Johnsson et al., 1987), where all C transformations are calculated according to first order rate kinetics, and nitrogen transformations are driven by carbon flows. The model consists of two residue pools; readily (litter 1) and slowly (litter 2) decomposable litter, one pool for microbial biomass, and one for humus. Carbon and N in each pool are considered separately. Each pool has a specific first order decay rate, decay meaning consumption by microorganisms (microbial biomass). The mineralization and assimilation of C and N during this microbial consumption are governed by the microbial growth yield efficiency factor (f_e), the humification coefficient (f_h) and the C:N ratio of new microbial biomass (r_0). If the substrate contains more N than that needed to obtain a microbial biomass C:N ratio (C/N_{mb}) equal to r_0, the N surplus is mineralized as NH_4-N (input to submodel 3, i.e. mineralized N is assumed to be instantly available on the residue layer–soil-interface). If the substrate contains less N than needed for $C/N_{mb} = r_0$, a net microbial N immobilization potential (N_{ImP}) is created. If there is not enough available inorganic N to match this potential (i.e. to obtain $C/N_{mb} = r_0$), the C:N ratio of the microbial biomass is allowed to increase accordingly. This increase in the C:N ratio of the microbial biomass was later used to regulate the decay rate of the slowly decomposing litter pool (see later in the text).

Assuming that ammonium is preferred over nitrate by the microbial biomass (Paul and Clark, 1989), and a Michaelis–Menten type uptake kinetic of N ions (Davidson and Hackler, 1994), the rate of immobilization of ammonium (N_{Im1}) and nitrate (N_{Im2}) is given by:

$$N_{Im1} = N_{ImP} \frac{C_1'}{C_1' + K_{s1}} \quad (1)$$

and

$$N_{Im2} = (N_{ImP} - N_{Im1}) \frac{C_2'}{C_2' + K_{s2}} \quad (2)$$

where C_1' and C_2' are the soil solution concentrations of NH_4–N and NO_3–N, respectively, and K_{s1} and K_{s2} are the half saturation constants, and N_{ImP} is the microbial N immobilization potential.

Submodel 3 has only three N pools; plant-N, NH_4–N and NO_3–N; carbon transformations are not included (Fig. 1). Concentration dependent processes are calculated after a discretization into a number (n) of sublayers of the soil (parallel to the straw and clover layers), i.e. the process rate is calculated for each sublayer individually for each time step. The clover and straw layers are not separated into sublayers. Thus the total number of layers is $n + 2$ (n sublayers of the soil plus one straw and one clover layer). The interface between residue layers and soil is located to sublayer number 1 and n (for clover and straw layers, respectively).

Mineralization of soil organic C and N is not included in the model; the measured rates were insignificant due to the low content of soil organic material (Wang and Bakken, 1997). Nitrification and transport are formulated in a set of two coupled partial differential equations (Darrah et al., 1983). The transport of ammonium and nitrate between the layers is simulated as diffusion in one dimension (perpendicular to layers), assuming that the concentration gradients (which drive the diffusion) would not have a component parallel to the layers (i.e. vertically or horizontally along the layers). Naturally, such concentration gradients parallel

to the layers may occur, but with minor importance for the competition between plant roots and microorganisms as a function of spatial separation of clover and straw layers. Mass flow along the axis perpendicular to the layers was assumed to be negligible, hence not modelled, due to the method of irrigation (frequent sprinkling of the whole soil surface) and the proliference of roots (pregerminated plant roots spread over the entire pot surface at planting).

The change in NH_4–N and NO_3–N concentrations with time in soil is given by:

$$\frac{\partial C_1'}{\partial t} = \frac{D_1 f\theta}{b}\frac{\partial^2 C_1'}{\partial x^2} + \frac{J_{\text{org-N}\leftrightarrow\text{NH}_4\text{–N}} - J_{\text{NH}_4\text{–N}\rightarrow\text{NO}_3\text{–N}} - J_{\text{NH}_4\text{–N}\rightarrow\text{Plant}}}{b} \quad (3)$$

$$\frac{\partial C_2'}{\partial t} = D_2 f\frac{\partial^2 C_2'}{\partial x^2} + \frac{-J_{\text{NO}_3\text{–N}\rightarrow\text{org-N}} + J_{\text{NH}_4\text{–N}\rightarrow\text{NO}_3\text{–N}} - J_{\text{NO}_3\text{–N}\rightarrow\text{Plant}}}{\theta} \quad (4)$$

D_1 and D_2 are diffusion coefficients in free solution of NH_4^+ and NO_3^-, respectively, f is the impedance factor reflecting the tortuosity of the diffusion pathway in the soil, θ the volumetric water content, x the distance (from clover layer surface), and b the buffer power for ammonium defined as the ratio of total NH_4^+ in the soil (not fixed) to NH_4^+ in solution (Darrah et al., 1983).

The Js represent sources and sinks for inorganic N: The first J term ($J_{\text{org-N}\leftrightarrow\text{NH4–N}}$, Eq. (3), and $J_{\text{NO}_3\text{–N}\rightarrow\text{org-N}}$, Eq. (4)) describes the microbial mineralization and assimilation (immobilization) of N, which occurs only in the clover and straw layers. These processes are controlled by submodels 1 and 2 (SOILN_NO). $J_{\text{org-N}\leftrightarrow\text{NH}_4\text{–N}}$ is either positive or negative depending on the substrate (positive in the clover layer and negative in the straw layer). $J_{\text{NO}_3\text{–N}\rightarrow\text{org-N}}$ is always positive (microbial assimilation of nitrate).

Nitrification, $J_{\text{NH}_4\text{–N}\rightarrow\text{NO}_3\text{–N}}$, is assumed to occur only in the soil layers. The nitrification rate is modelled as (Darrah et al., 1983):

$$J_{\text{NH}_4\text{–N}\rightarrow\text{NO}_3\text{–N}} = \frac{\mu m}{Y} \quad (5)$$

where m is the number of ammonium oxidizing bacteria per unit volume soil, μ is their growth rate as a function of ammonium concentration (see Eq. (7)) and Y is their growth yield, i.e. the number of ammonium oxidizers formed per unit of NO_3–N produced. We further assumed logistic growth of the ammonia oxidizers in order to be able to set an upper limit for the population growth:

$$\frac{\mathrm{d}m}{\mathrm{d}t} = \mu m\left(1 - \frac{m}{K}\right) \quad (6)$$

where K is the maximal number of ammonium oxidizers per unit volume soil ("carrying capacity") and μ is assumed to be controlled by the substrate concentration (Darrah et al., 1983):

$$\mu = \mu_{\max}\frac{C_1'}{C_1' + K_{s\mu}} \quad (7)$$

where $\mu_{\max}$ is the maximum growth rate and $K_{s\mu}$ is the half saturation constant.

The last J term in both Eqs. (3) and (4) describe the plant N uptake. Plant N uptake is described on the assumptions that (i) plant roots were evenly distributed, (ii) that plants prefer nitrate over ammonium (Haynes, 1986) and (iii) that the plant N demand (N_{demand}) can be described as a linear function of time (since only a short growth period early in the plant development is to be modelled in this experiment):

$$N_{\text{demand}} = N_{d0} + k_p t \quad (8)$$

where N_{d0} is the initial demand and k_p is a slope constant. N demand is assumed to be equal in the n sublayers, and the actual uptake is calculated separately for each layer. Two mechanisms for N uptake are built into the model; passive uptake of NO_3–N via the mass flow driven by transpiration, and active uptake of NO_3–N and NH_4–N after diffusion to the roots and enzymatic processes. The rate of NO_3–N uptake from each soil sublayer (i) due to transpiration is described by:

$$J_{\text{NO}_3\text{–N}\rightarrow\text{Plant,mf}(i)} = C_{2(i)}' T \quad (9)$$

where $J_{\text{NO}_3\text{–N}\rightarrow\text{Plant,mf}(i)}$ is the nitrate uptake by mass flow in sublayer i, $C_{2(i)}'$ is the concentration of NO_3–N in the soil solution in sublayer i and T is the transpiration rate per unit of soil (ml cm^{-3} d^{-1}). Based on daily measurements of transpiration by weighing of the pots prior to watering (J. Wang, unpublished), T is calculated as:

$$T = (50 + 2.5t)10^{-5} \quad (10)$$

where t is the time in days.

The active uptake of inorganic N was then assumed to follow Michaelis–Menten kinetics (Breteler and Nissen, 1982; Nissen, 1973), and the total uptake rate of NO_3–N from each soil sublayer (i) is therefore given by:

$$J_{\text{NO}_3\text{–N}\rightarrow\text{Plant}(i)} = (N_{\text{demand}(i)} - J_{\text{NO}_3\text{–N}\rightarrow\text{Plant,mf}(i)})\frac{C_{2(i)}'}{C_{2(i)}' + K_{s2p}} + J_{\text{NO}_3\text{–N}\rightarrow\text{Plant,mf}(i)} \quad (11)$$

where $J_{\text{NO}_3\text{–N}\rightarrow\text{Plant}(i)}$ is the nitrate uptake from sublayer i, K_{s2p} is the half saturation constant for active NO_3–N uptake in plants, the other variables are explained previously. The uptake rate of NH_4–N is then calculated as a function of the remaining plant N demand (after NO_3–N uptake has been calculated) and the concentration of NH_4–N

Table 1
Pre-set parameter values used in the model

Parameter	Value	Unit	Ref.	Description
k_1	0.13	d^{-1}	Vold et al. (1999)	Specific decay rate of readily decomposable litter (litter 1)
k_2	0.05	d^{-1}	Vold et al. (1999)	Specific decay rate of slowly decomposable litter (litter 2)
k_h	7.2×10^{-5}	d^{-1}	Vold et al. (1999)	Specific decay rate of humus
r_0	5.3	–	Vold et al. (1999)	C:N ratio of new biomass when nitrogen is unlimiting
D_1	1.9×10^{-5}	$cm^2\ s^{-1}$	Robinson and Stokes (1959)	Diffusion coefficient of NO_3^- in free solution
D_2	1.96×10^{-5}	$cm^2\ s^{-1}$	Robinson and Stokes (1959)	Diffusion coefficient of NH_4^+ in free solution
θ	0.22	$ml\ cm^{-3}$	Vold et al. (1999)	Volumetric water content
f	0.45[a]	–	Nye (1979)	Impedance factor
μ_{max}	1.1×10^{-2}	h^{-1}	Jiang and Bakken (1999)	Maximum growth rate of ammonium oxidizers
$k_{s\mu}$	1.1e − 5	$g\ g^{-1}$	Jiang and Bakken (1999)	Half saturation constant for specific growth rate of ammonium oxidizers
Y	$1.3 \times 10^{+11}$	cells g^{-1} NH_4–N	Jiang and Bakken (1999)	Growth yield of ammonium oxidizers
K_{s1p}	5.2×10^{-6}	$g\ ml^{-1}$	Nissen (1973)	Half saturation constant for NH_4–N uptake in plant roots
K_{s2p}	1.4×10^{-8}	$g\ ml^{-1}$	Breteler and Nissen (1982)	Half saturation constant for NO_3–N uptake in plant roots

[a] Calculated from the theoretical relationship: $f = \theta^{0.5}$.

in each layer:

$$J_{NH_4\text{–}N\rightarrow Plant(i)} = (N_{demand(i)} - J_{NO_3\text{–}N\rightarrow Plant(i)}) \frac{C'_{1(i)}}{C'_{1(i)} + K_{s1p}} \quad (12)$$

where K_{s1p} is the half saturation constant for the active NH_4–N uptake in plants.

The number of sublayers (n) was set to 20 for all simulations. As an approximation of the second derivatives in Eqs. (3) and (4) the central difference is used, i.e.

$$\frac{\partial^2 C_i}{\partial x^2} \approx \frac{C_{i-1} - 2C_i + C_{i+1}}{(\Delta x)^2} \quad (13)$$

This gives 40 ordinary differential equations (ODEs). In submodel 1 and 2 the turnover of the four C- and N pools (litter 1 and 2, humus and biomass) is described by 16 ODEs. Together the equations comprise a set of coupled ODEs, which are solved with a variable order Runge–Kutta method in MATLAB 5.3 (relative error of 10^{-3}). Reducing the relative error or increasing the number of sublayers did not alter the results significantly.

2.3. Model calibration

Some model parameters were set according to literature values (Table 1), and the subdivision of the plant material into litter pools (Table 2) was based on previous experiments (Henriksen and Breland, 1999), in which the degradability of similar plant materials was investigated by stepwise chemical digestion (Goering and van Soest, 1970). Readily (litter 1) and slowly (litter 2) decomposable plant material is equivalent to the neutral detergent soluble and the cellulose and hemicellulose like fractions, respectively. The resistant fraction of the plant material (equivalent to the lignin fraction) was placed in the humus pool of the model. The other initial values listed in Table 2 are based on measured values (Wang and Bakken, 1997).

The remaining model parameters were estimated step by step (A–D, Table 3) by minimizing the squared residuals between simulations and selected parts of the experimental data using the Nelder–Mead algorithm (Whitmore, 1991). To evaluate the model performance quantitatively we calculated the root mean squares error (RMSE), the modelling efficiency (EF), the coefficient of determination (CD) (Mayer and Butler, 1993), and the t-statistic (t) of the mean difference (Smith et al., 1997). A t-value less than the critical two-tailed 2.5% t value was taken to indicate that the simulation showed no significant (n.s.) bias towards over- or underestimation when compared to measured values (i.e. no significant difference between simulated and measured values). The parameters estimated in one step were kept unaltered in subsequent simulations. This procedure implies that model parameterization and evaluation is using very closely related experiments. This is justifiable, since we are using the model as an explanatory tool only, and not predictively. The steps and the results of these calibrations are summarized in Table 3.

In step A (Table 3), the data for measured organic N in clover layers (12 mm treatments) were used to estimate three parameters which control the coupling between microbial C- and N transformations; the decay rate and growth yield of the microbial biomass (k_b and f_e) and the humification coefficient (f_h, i.e. the fraction of microbially assimilated C and N which is turned into humus). The residuals (squared) to be minimized were the differences between measured organic N in clover layers and the simulated organic N (i.e. residual clover N + microbial biomass-N + humus-N). The statistics for the final parameter setting in step A (evaluating the model fit to the calibration data) were: RMSE = 4.559, EF = 0.935, CD = 0.937 and t = 0.251 (n.s.).

In step B we estimated the nitrification parameter K and the initial numbers of ammonium oxidizing bacteria, m_0, using measured NO_3–N content at days 14, 21 and 28 in a control pot amended with clover only (J. Wang, PhD thesis,

Table 2
Initial C and N pools in clover, straw and soil, and initial plant N content

Variable	Value (mg pot^{-1})		Description
	C	N	
Clover residues[a]			
Litter 1	577.0	59.5	C and N content in readily decomposable fraction of clover residues
Litter 2	338.9	13.1	C and N content in slowly decomposable fraction of clover residues
Humus	38.2	3.0	C and N content in very slowly decomposable fraction of clover residues
Biomass	1.0×10^{-3}[b]	1.0×10^{-4}[b]	C and N content in microbial biomass decomposing clover residues
Straw[a]			
Litter 1	275.7	8.3	C and N content in readily decomposable fraction of straw
Litter 2	1562.1	13.9	C and N content in slowly decomposable fraction of straw
Humus	227.2	3.0	C and N content in very slowly decomposable fraction of straw
Biomass	1.0×10^{-3}[b]	1.0×10^{-4}[b]	C and N content in microbial biomass decomposing straw
Soil			
C_1		1.0×10^{-5}[c]	Concentration of NH_4-N in whole soil
C_2		1.0×10^{-5}[c]	Concentration of NO_3-N in whole soil
Plant			
Plant N		2.02	N content in plant

[a] Sub-division of the plant material based on literature data (Henriksen and Breland, 1999).
[b] The values were set.
[c] Below detection limit.

Agricultural University of Norway, 1991). The statistics for the final parameter setting in step B were: RMSE = 6.869, EF = 0.992, CD = 0.993, $t = -0.264$ (n.s.).

In step C, we first used the data for inorganic N in U3 (i.e. pots without plants, 3 mm distance) to estimate half saturation coefficients for microbial ammonium and nitrate assimilation (K_{s1}, K_{s2}) and the soil buffer power (b). In these simulations, however, C/N_{mb} (i.e. the C:N ratio of the microbial biomass) in the straw layers reached values larger than 35, which is unreasonably high (Van Veen et al., 1984). A rate modifying factor (a) was therefore applied to the decay rate coefficient for slowly decomposing litter (k_2) so as to let available N, indirectly expressed by the microbial biomass C:N ratio (C/N_{mb}), regulate the activity of enzymes hydrolyzing structural plant components (i.e. slowly decomposable litter) as suggested by Henriksen and Breland (1999):

$$k_2' = ak_2 \tag{14}$$

where k_2' is the modified decay rate constant for slowly decomposable litter and a is given by:

$$a = \frac{r_{max} - C/N_{mb}}{r_{max} - r_0}, \quad 0 \le a \le 1 \tag{15}$$

where r_{max} is the maximum C:N ratio of the microbial biomass (C/N_{mb}) for litter 2 decomposition. The value of a is in the range 0–1, since r_0 is the lower limit of C/N_{mb}. The estimation of r_{max} was then included in the parameter estimation step C, as shown in Table 3. (RMSE = 6.391, EF = 0.979, CD = 0.980, $t = -0.472$ (n.s.)).

In the last calibration step, D, the initial plant N demand (N_{d0}) and the slope of increase of this demand (k_p) were estimated using plant N and inorganic N data from P3 (RMSE = 9.053, EF = 0.917, CD = 0.921, $t = 0.152$ (n.s.)).

3. Results and discussion

3.1. Simulations of N-dynamic in pots without plants

The model simulated the measured content of soil inorganic N (N_{min}) in the U6, U9 and U12 treatments efficiently (Table 4). Approximately 71% of the variation in the measurements could be described by the model (Table 4, Fig. 2). The observed increase in soil inorganic N concentrations with increasing distance between N sources and sinks in the unplanted pots (Wang and Bakken, 1997) was thus well simulated by the model.

Our assumption that diffusion of inorganic N ions in the soil solution was the major transport process in the unplanted pots appears reasonable, but other hypotheses should briefly be mentioned. Active transport of nitrogen through fungal hyphae is potentially more effective than diffusion of ammonium through the soil water phase. Based on McLean and Prosser (1987), who found hyphal extension rates of the fungus *Neurospora crassa* to range from 200 $\mu m\,h^{-1}$ (secondary branches) to 1400 $\mu m\,h^{-1}$ (leading hyphae), the estimated time for hyphae to cross the longest distance between the clover and straw layers in our simulations (12 mm) would be less than three days. A "bypass" through fungal hyphae between the clover and the straw layers could therefore theoretically be established in the early stage of the experiment. Wang and Bakken (1997) recorded sparse growth of fungi however, suggesting

Table 3
Parameter values estimated by minimization of the sum of squared residuals between model simulations and different data sets

	Initial value	Unit	Ref.	Estimated value[a]	Descriptions
Step A					
k_b	1.0×10^{-2}	d^{-1}	Vold et al. (1999)	1.2×10^{-1}	Specific decay rate of microbial biomass
f_e	0.3	–	Vold et al. (1999)	0.5	Microbial growth yield efficiency
f_h	0.11	–	Vold et al. (1999)	0.2	Humification coefficient
Step B					
K	$1.1\times10^{+7}$	Cells cm^{-3}	Bender and Conrad (1994); Jiang and Bakken (1999)	$2.0\times10^{+7}$	Carrying capacity for ammonium oxidizers
m_0	$1.0\times10^{+4}$	Cells cm^{-3}	Set	$8.8\times10^{+5}$	Initial number of ammonium oxidizers
Step C					
K_{s1}	1.0×10^{-6}	g ml^{-1}	Van Veen et al. (1984)	8.2×10^{-6}	Half saturation constant for NH_4–N immobilization
K_{s2}	1.0×10^{-6}	g ml^{-1}	Van Veen et al. (1984)	3.4×10^{-6}	Half saturation constant for NO_3–N immobilization
B	9	[b]	Kirk and Solivas (1997)	8	Soil buffer power
r_{max}	15	–	Van Veen et al. (1984)	9	Maximum C:N ratio of microbial biomass for litter 2 decomposition
Step D					
N_{d0}	4.04×10^{-5}	g cm^{-3} d^{-1}	Set	7.07×10^{-5}	Initial plant N demand
k_p	1.0×10^{-8}	g cm^{-3} d^{-2}	Set	2.2×10^{-8}	Slope constant for plant N demand

[a] Residual sum of squares (Whitmore, 1991) minimized using the Nelder–Mead algorithm. The parameters set in one step were kept unaltered in subsequent steps.
[b] Unit: g cm^{-3} (soil + solution)/g ml^{-1} (solution).

that this transport may have been of minor importance. In undisturbed soil, an established network of fungal hyphae could be of great importance, however.

The model tended to underestimate the N_{min} content in U9, and relative large residuals were found in U6 and U12 at day 14 and 21, respectively (Fig. 2). We cannot explain the tendency for underestimation in U9. We speculate that measuring errors in U6 and U12 may explain the marked deviations for single data points.

The mixed treatments could not be simulated along with the others, since we did not know the distance between clover and straw particles (x) for these treatments. However, we estimated x by using data from UMIX and applying the same optimization procedure as used when calibrating the model. An average distance of 1.2 mm gave the best fit to data (RMSE = 43.502, EF = 0.603, CD = 0.923, t = 0.644 (n.s.)), although the residual on day 14 was quite large (Fig. 3). The simulated plant N uptake with this distance (1.2 mm) is somewhat higher than measured values (Fig. 3, see also Fig. 7).

Table 4
Root mean squares error (RMSE), modelling efficiency (EF), coefficient of determination (CD) and t-statistic (t) of the mean difference for the simulations of the independent treatments (i.e. not used for calibrations). The contents of soil inorganic N and plant N (mg N pot^{-1}) were used as response for unplanted (U) and planted treatments (P), respectively

Treatments[a]	RMSE	EF	CD	t[b]
U6,U9,U12	35.096	0.611	0.707	−0.302 (n.s.)
P6,P9,P12	11.633	0.860	0.937	1.503 (n.s)

[a] Numbers indicate distance (mm) between hotspots.
[b] $\alpha = 0.05$, n.s. = not significant difference between simulated and measured.

Fig. 4 illustrates the simulated changes in NH_4–N and NO_3–N concentrations as a function of time and position (i.e. the position between clover and straw layer) for U12. At the clover surface (i.e. at 0 mm in Fig. 4), the simulated concentrations of NH_4–N and NO_3–N reached a maximum at day 15 and at day 30, respectively. Ammonium shows steeper gradients than nitrate, both along the time and the space axis, reflecting the slower diffusion of ammonium and the fact that ammonium production precedes and its rate necessarily exceeds the nitrate production. Inhibition of nitrification may occur by high concentrations of NH_4–N (Darrah et al., 1985). We did not include in the model any mechanism for such inhibition, and this appeared to be justified by the relatively low simulated (and measured) concentrations of NH_4–N (<0.75 μmol g^{-1} soil).

Our simulated NH_4–N concentrations declined rapidly after reaching maximum values at day 15, while NO_3–N concentrations seemed to be more stable towards the end of the experiment (Fig. 4). Calculated from the results in Fig. 4, approximately 60% of the total inorganic N should be NO_3–N by day 42. This is in accordance with Wang (unpublished), who measured the content of NH_4–N and NO_3–N in thin sections including both the clover layer and the surrounding soil from U9 and U12 (Fig. 5). The simulation output could not be tested statistically, but the figure shows convincing simulation of nitrification.

3.2. Simulations of N-dynamics in pots with competition between microorganisms and plants

The model simulated plant N uptake very well (Fig. 6). The simulations showed no bias towards over- or underestimation of the measurements for the P6, P9 and P12, and

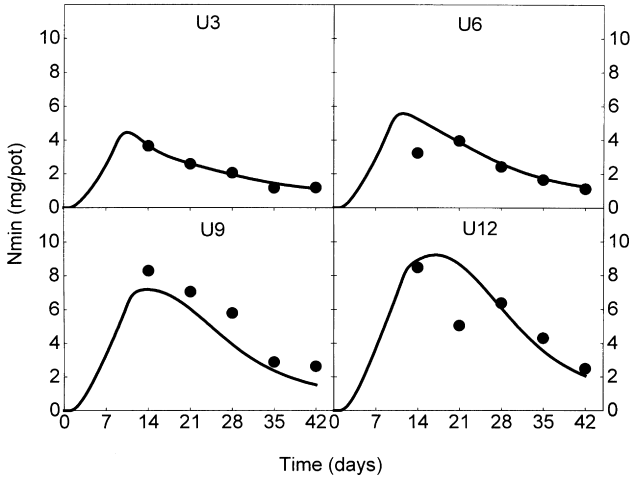

Fig. 2. Measured (symbols) and simulated (lines) content of soil inorganic N (N_{min}) for unplanted pots (U indicates unplanted, the number indicates the distance in mm between hotspots). Note that U3 was used to calibrate the model.

about 94% of the variation between data was adequately described by the model (Table 4). There were small differences in total plant N content between treatments. Wang and Bakken (1997) took their experimental results to suggest that there was a critical distance between 3 and 6 mm, above which plants obtained no extra N. This was not matched by the model results; the simulated plant content at day 42 increased over the whole range of distances (Fig. 7). In fact, the presentation of both experimental data and simulations in Fig. 7 lends little support to the conclusion reached by Wang and Bakken (1997). In our opinion, this is a good example of how dynamic modelling of experimental

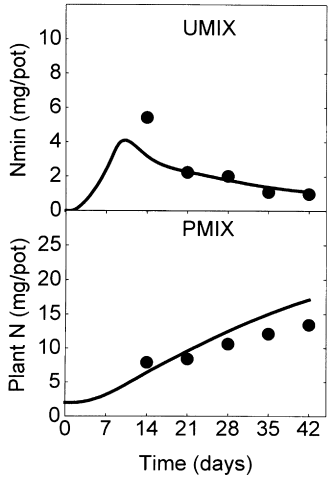

Fig. 3. Measured (symbols) and simulated (lines) for pots where clover and straw was mixed evenly into the soil. The figure shows inorganic N in the unplanted pots (UMIX) and plant N for the planted pots (PMIX). The simulations are based on an estimated distance of 1.2 mm between hotspots (clover and straw particles), which was the distance that minimized residuals for the UMIX data.

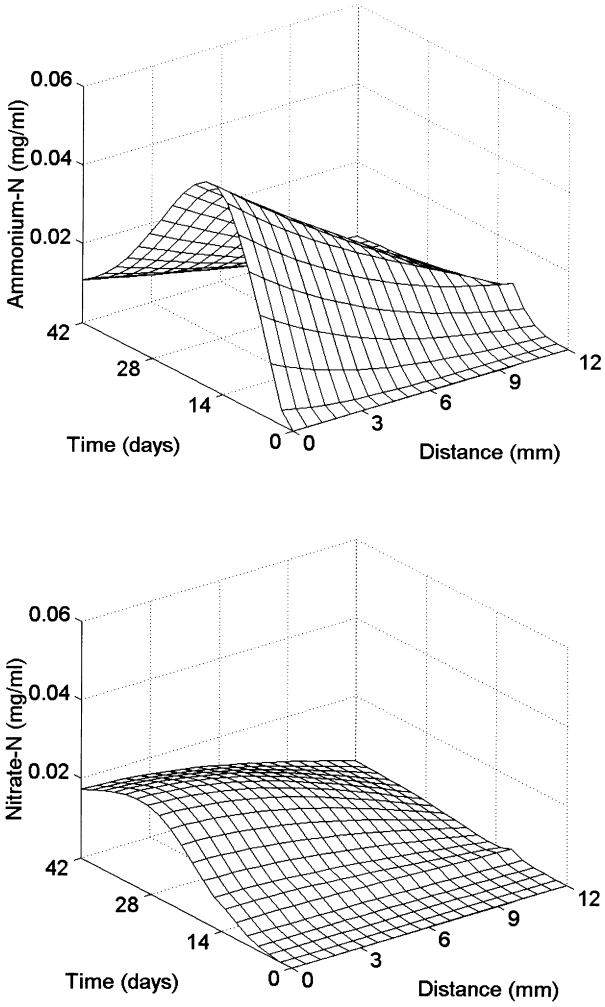

Fig. 4. Simulated concentrations of ammonium-N (upper figure) and nitrate-N (lower figure) in unplanted pots with 12 mm distance between hotspots (U12) as a function of time and position in the soil layer separating the clover residues (at 0 mm) and straw (at 12 mm).

results can help avoiding incorrect interpretations of experimental data.

The simulated (and measured) soil NO_3–N concentrations were very small in the planted pots compared to the unplanted ones (data not shown). We attribute the low concentrations of NO_3–N partly to efficient plant uptake of both NO_3 and NH_4 (uptake of NH_4 reducing the nitrification). This is in accordance with Hook et al. (1991) who measured a smaller nitrate to ammonium ratio in soil with plant cover than in soil from openings (i.e. no plant roots present), in North American short grass steppe.

3.3. Sensitivity test of the model

A sensitivity test was performed in order to examine the effect of ±10% changes in parameter values. To describe the sensitivity, we decided to inspect the response of four model estimates: the inorganic N content in U3 and U12 at day 14 ($N_{soil,\,14}$) and plant-N in P3 and P12 at day 42 ($N_{plant,\,42}$).

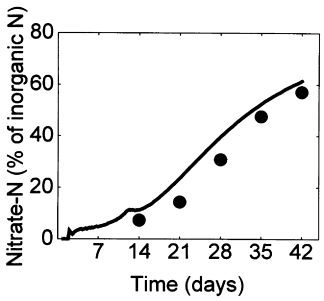

Fig. 5. Measured (symbols) fraction of nitrate-N (of inorganic-N) in the soil surrounding the clover layers as an average for U9 and U12 (U indicates unplanted, the number indicates the distance in mm between hotspots) (J. Wang, unpublished) and simulated (line) fraction of nitrate-N surrounding the clover layers (sublayer 1) at U12.

The rationale for choosing these model estimates was that the effect of soil layer thickness was most pronounced here. The result of the sensitivity test is shown in Table 5, as the percent change of each of the four estimates in response to a 10% change (+ and −) for each parameter value.

In general, the analysis showed that the model estimates were sensitive only to the parameters that regulated the microbial C and N transformations. Not surprisingly, the net mineralization of N increased substantially in response to a reduction in growth efficiency (f_e) and an increased C:N ratio of new microbial biomass (r_0). Together with the humification coefficient (f_h), these parameters regulate the partitioning of C and N between mineralization, assimilation and production of stable organic materials (humus), thus strongly affecting the net mineralization in the clover layers (which thus regulates "up-stream" in relation to the diffusion and competition for inorganic N). A blatant deviation from the plausible responses to the mentioned parameters is the increase in inorganic N in U3 when the growth efficiency of microorganisms (f_e) was increased. A closer inspection of the responses to this change revealed that the 10% increase in f_e resulted in a prolongation of a transient retardation of litter 2 degradation (not shown) due to the high C:N ratio of the microbial biomass (Eq. (15)). This delayed the immobilization based on litter 2 and resulted in a transient increase in the inorganic N level of U3.

The decomposition coefficients for litter (k_1 and k_2), humus (k_h) and microbial biomass (k_b) had slight but fairly obvious effects with some exceptions: By increasing the decay rate of stable litter (k_2), the inorganic N levels were reduced (and vice versa). This suggests an effect of synchronizing between mineralization in the clover layers and immobilization (dominated by litter 2) in the straw layers (increasing the k_2 improved synchronization, hence improving microbial capturing of mineralized N). Another unexpected effect was the reduced inorganic N level in U3 by increasing the decay rate of microorganisms (k_b). As for the U3 response to f_e (see above), we found the cause to this response to be the control of the litter 2 decay by the microbial biomass C:N ratio (increased decay rate of microorganisms resulted in an earlier reduction in the biomass C:N ratio, hence an earlier recovery of the litter 2 degradation (Eq. (15)), hence a more efficient immobilization).

Apart from anomalies mentioned, the decomposition parameter responses for the inorganic N (U3 and U12) were congruent with those of plant-N (P3 and P12); i.e. the parameter changes that increased the inorganic N in unplanted pots did also increase plant N uptake. In contrast, the nitrification parameters gave consistently incongruent response patterns: increased nitrification rates (m, μ_{max} or V_{max}) reduced inorganic N (U3 and U12), but it increased the plant N in P3 and P12, and vice versa. The reason for this is that the substrate half saturation constant for NO_3 uptake by plant roots (1.4×10^{-8}) was more than two orders of

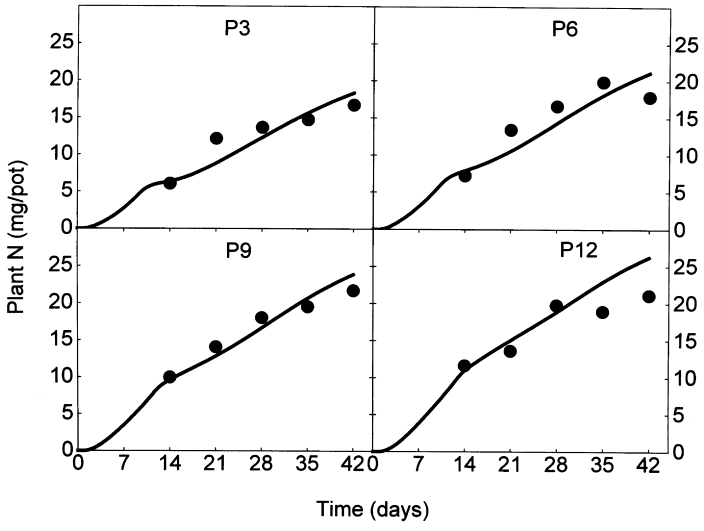

Fig. 6. Measured (symbols) and simulated (lines) content of plant N for planted pots (P indicates planted, the number indicates the distance in mm between hotspots). Note that P3 was used to calibrate the model.

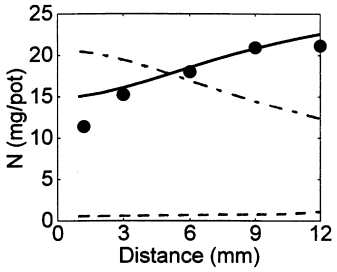

Fig. 7. Measured (symbols) and simulated effects of distance between hotspots (clover and straw) on the content of plant N (initial N content subtracted) (—), and simulated content of N immobilized (by straw decomposers) (· - ·) and soil inorganic N (- -) at day 42.

magnitude lower than the other inorganic N substrate half saturation constants (520, 820 and 340 10^{-8}, for plant ammonium, microbial ammonium and microbial nitrate uptake, respectively). Thus increased nitrification enabled plants to capture more inorganic N. In the unplanted pots, however, increased nitrification reduced the inorganic N level since nitrate diffused faster to the straw layers (to become immobilized) than did ammonium.

The simulated plant N content was most sensitive to N_{d0} and insensitive to k_p and K_{s1p}. In general, plant N was insensitive to parameters regulating processes involving nitrate-N (K_{s2}, K_{s2p}, nitrification parameters). This may be explained by the low simulated concentrations of NO_3–N discussed in the previous section.

3.4. Conclusions

The model successfully simulated the competition between plants and microorganisms for inorganic N and the dependency of this competition on spatial heterogeneity. This lends support to the previous interpretation (Wang and Bakken, 1997) that plant roots will increase the net microbial N mineralization in soil, not by stimulating the microbial activity but by successfully inflicting N starvation on soil microorganisms. It strongly suggests that conflicting results regarding the competitiveness of plant roots versus microorganisms (Kaye and Hart, 1997) could be due to differences in spatial heterogeneity of the soil matrix.

The model exercise shows that spatio-temporal segregation of microbial net mineralization and immobilization in

Table 5
The relative change of simulated soil N content at day 14 ($N_{soil,\ 14}$) for unplanted pots with 3 mm (U3) and 12 mm (U12) distance between hotspots and simulated plant N at day 42 ($N_{plant,\ 42}$) for planted pots with 3 mm (P3) and 12 mm (P12) distance between hotspots when values of parameters are increased or decreased separately by 10%. The original parameter values are those given in Tables 1 and 2

Parameter	Change in $N_{soil,\ 14}$ (%)				Change in $N_{plant,\ 42}$ (%)			
	U3		U12		P3		P12	
	+10%	−10%	+10%	−10%	+10%	−10%	+10%	−10%
Decomposition								
k_1	1	−1	4	−5	+0	−1	1	−1
k_2	−3	4	−1	1	−1	1	−0	+0
k_h	0	0	+0	−0	+0	−0	+0	−0
k_b	−2	5	5	−5	+0	−0	1	−1
f_e	29	8	−31	19	−11	13	−11	9
f_h	−2	2	−3	3	−3	3	−2	2
r_0	22	−5	17	−20	15	−15	8	−10
r_{max}	−20	47	−6	15	−5	−8	−2	2
K_{s1}	9	−10	2	−2	3	−3	1	−1
K_{s2}	+0	−0	+0	−0	+0	−0	+0	−0
Diffusion								
F	−1	2	−3	4	−1	1	−1	1
B	11	−11	5	−5	−0	+0	−0	+0
Nitrification								
K	−0	+0	−0	+0	+0	−0	1	−1
M_0[a]	−2	2	−1	1	1	−1	+0	−0
μ_{max}	−1	1	−1	1	1	−1	1	−1
$K_{s\mu}$	1	−2	1	−1	−1	2	−1	1
V_{max}	−2	2	−1	1	1	−1	1	−1
Plant N uptake								
N_{d0}[a]	–	–	–	–	5	−5	5	−5
k_p	–	–	–	–	+0	−0	+0	−0
K_{s1p}	–	–	–	–	−2	2	−1	1
K_{s2p}	–	–	–	–	−0	+0	−0	+0

[a] Initial value.

Table A1

Parameter	Description	Unit	Category
θ	Volumetric water content	ml cm^{-3}	Parameter
μ	Specific growth rate of ammonia oxidizers	H^{-1}	Parameter
μ_{max}	Maximum growth rate of ammonium oxidizers	H^{-1}	Parameter
a	Modifying factor of k_2	–	Variable
b	Soil buffer power	g cm^{-3}/g ml^{-1}	Parameter
C/N_{mb}	C:N ratio of microbial biomass	–	Variable
C_1	NH_4–N concentration in whole soil (soil + solution)	g cm^{-3}	Variable
C_1'	NH_4–N concentration in soil solution	g ml^{-1}	Variable
C_2	NO_3–N concentration in whole soil (soil + solution)	g cm^{-3}	Variable
C_2'	NO_3–N concentration in soil solution	g ml^{-1}	Variable
D_1	Diffusion coefficient of NO_3^- in free solution	cm^2 s^{-1}	Parameter
D_2	Diffusion coefficient of NH_4^+ in free solution	cm^2 s^{-1}	Parameter
f	Impedance factor	–	Parameter
f_e	Microbial growth yield efficiency	–	Parameter
f_h	Humification coefficient	–	Parameter
$J_{NH_4–N→NO_3–N}$	Nitrification rate	g cm^{-3} s^{-1}	Flow variable
$J_{NH_4–N→Plant}$	NH_4–N uptake rate in plants	g cm^{-3} s^{-1}	Flow variable
$J_{NO_3–N→org–N}$	NO_3–N immobilization rate	g cm^{-3} s^{-1}	Flow variable
$J_{NO_3–N→Plant}$	NO_3–N uptake rate in plants	g cm^{-3} s^{-1}	Flow variable
$J_{NO_3–N→Plant,mf}$	NO_3–N uptake rate in plants via massflow	g cm^{-3} s^{-1}	Flow variable
$J_{org–N↔NH_4–N}$	NH_4–N mineralization/immobilization rate	g cm^{-3} s^{-1}	Flow variable
K	Carrying capacity for ammonium oxidizers	cells cm^{-3}	Parameter
k_1	Specific decay rate of readily decomposable litter	D^{-1}	Parameter
k_2	Specific decay rate of slowly decomposable litter	d^{-1}	Parameter
k_2'	Modified decay rate of slowly decomposable litter	D^{-1}	Variable
k_b	Specific decay rate of microbial biomass	D^{-1}	Parameter
k_h	Specific decay rate of humus	D^{-1}	Parameter
k_p	Slope constant for plant N demand	g cm^{-3} d^{-2}	Parameter
$k_{s\mu}$	Half saturation constant for specific growth rate of ammonium oxidizers	g ml^{-1}	Parameter
K_{s1}	Half saturation constant for NH_4–N immobilization	g ml^{-1}	Parameter
K_{s1p}	Half saturation constant for NH_4–N uptake in plant roots	g ml^{-1}	Parameter
K_{s2}	Half saturation constant for NO_3–N immobilization	g ml^{-1}	Parameter
K_{s2p}	Half saturation constant for NO_3–N uptake in plant roots	g ml^{-1}	Parameter
m	Number of ammonia oxidizers	cells cm^{-3}	State, internal
m_0	Initial number of ammonium oxidizers	cells cm^{-3}	State, initial
N_{d0}	Initial plant N demand	g cm^{-3} d^{-1}	State, initial
N_{demand}	Plant N demand	g cm^{-3} d^{-1}	Variable
N_{Im1}	Immobilization rate of ammonium	g d^{-1}	Variable
N_{Im2}	Immobilization rate of nitrate	g d^{-1}	Variable
N_{ImP}	N immobilization potential	g d^{-1}	Variable
r_{max}	Maximum C:N ratio of microbial biomass for litter 2 decomposition	–	Parameter
r_0	C:N ratio of new biomass when nitrogen is unlimiting	–	Parameter
T	Specific volumetric transpiration rate	ml cm^{-3} d^{-1}	Variable
x	Distance between N sources and microbial sinks	mm	Parameter
Y	Growth yield of ammonium oxidizers	cells g^{-1} NH_4–N	Parameter

the soil matrix has profound implications not only for plant N uptake, but also for the physiological status on the saprophytic soil community. Severe and persistent N starvation inflicted by the presence of active roots may retard the degradation of polymeric materials (Wang and Bakken, 1997). The growth restrictions inflicted by the N starvation are likely to affect the partitioning of available C substrates (uncoupled respiration, production of PHA, exudation and production of extracellular polymers). Unfortunately, very little is known about the physiology of N starvation of soil microorganisms. This clearly deserves more attention in the future. Molecular biology holds a store of promising techniques for testing for and localizing N starved organisms (reporter genes and reporter organisms) as well as for studying the regulation of cell metabolism during N starvation. The physiology of N starvation of microorganisms may reveal new aspects of the "stoechiometry" of microbial C and N transformations in soil, with implications for the long-term changes in the C:N ratio of stabilized organic matter in the soil.

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Appendix A

The list of symbols sorted by symbol names (unit of soil buffer power: g cm^{-3} (soil + solution)/g ml^{-1} (solution)) is shown in Table A1.

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