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EXPERIMENTAL ARTICLES

Mathematical Simulation of the Dynamics of Interacting Populations of Rhizosphere Microorganisms

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Abstract—A quantitative model is proposed to describe the population dynamics of associative nitrogen-fixing microorganisms in the plant rhizosphere as dependent on the rate of carbon substrate exudation by plant roots. By changing the values of the basic model parameters, the effect of various factors on the behavior of two competing populations of rhizosphere microorganisms can be studied.

Key words: mathematical model, associative nitrogen fixers, carbon substrate, rhizosphere.

Mathematical models simulating the population dynamics of soil microorganisms in the plant root zone are fairly common in the literature. Most of them are concerned with the behavior of an undifferentiated microbial community as a function of a single external factor—the concentration in the rhizosphere of soluble organic compounds [1–4].

In view of the large number of factors affecting the growth and activities of associative nitrogen-fixing bacteria, it would be interesting to have a mathematical model describing the dynamics of their development on plant roots and in rhizosphere soil. In addition to evaluating the energy requirements to sustain the activities of a nitrogen-fixing population, it would be important to estimate the influence of other soil factors and land-treatment practices on this process. However, there are virtually no publications concerned with mathematical simulation of the population dynamics of soil nitrogen-fixing microorganisms. Previously, we proposed a simulation model of associative nitrogen fixation in the rhizosphere of nonleguminous cultures [5]. In this model, the population variation of free-living nitrogen-fixing bacteria and the competing rhizosphere microflora under the influence of three external factors is described by a set of four ordinary differential equations of the first order.

The purpose of this work was to modify the previous model on the basis of biological evidence in order to describe the population dynamics of nitrogen-fixing bacteria in the plant rhizosphere as determined by the rate of carbon substrate release by the roots, the competition with the nonfixing microflora, and the concentrations of nitrogen and oxygen in the rhizosphere.

RESULTS AND DISCUSSION

The plant–soil–soil microflora system should be considered as a diffusion system with multiple and complex links among its spatially distributed components [6].

The model is represented by the following set of differential equations, each one describing a separate variable of the process:

$$\begin{cases} \dfrac{dX_A}{dt} = X_A[\mu_A(S, P) - d_A] \\ \dfrac{dX_K}{dt} = X_K[\mu_K(S, P) - d_K] \\ \dfrac{dS}{dt} = -q_{SA}X_A - q_{SK}X_K - V_{DS} + V_S + L_S \\ \dfrac{dP}{dt} = -q_{PA}X_A - q_{PK}X_K - V_R + V_P - L_P, \end{cases} \quad (1)$$

where X_A and X_K are, respectively, the biomasses of the nitrogen-fixing and competing nonfixing microorganisms per unit volume of rhizosphere soil and S and P are the concentrations in soil of the specific organic substrate and dissolved oxygen, respectively. In these equations, μ_A and μ_K are the specific rates of multiplication of the nitrogen-fixing and competing microorganisms; d_A and d_K are the specific death rates of the nitrogen-fixing and competing microorganisms; q_{SA}, q_{SK}, q_{PA}, and q_{PK} are, respectively, the specific metabolic coefficients of organic substrate and oxygen utilization by the nitrogen-fixing and competing microorganisms; L_S and L_P are, respectively, the rates of substrate exudation and oxygen uptake in a unit soil volume; V_S and V_{DS}

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are, respectively, the rates of diffusion inflow and outflow of the organic substrate released by roots in a unit volume of rhizosphere soil; and V_P and V_R are, respectively, the rate of diffusion influx of oxygen into a unit volume of rhizosphere soil and the rate of oxygen utilization by the root system.

The specific multiplication rates μ_A and μ_K are functions of the substrate and oxygen content of the rhizosphere, while the metabolic coefficients q_{SA}, q_{SK}, q_{PA}, and q_{PK} are functions of the specific multiplication rates. The diffusion rates V_{DS}, V_P, and V_R are determined by the diffusion constants for the substrate and oxygen, by their concentration gradients in the rhizosphere, and by the geometric dimensions of the latter. The rate of root exudation substrate inflow V_S into a unit volume of rhizosphere soil is approximated by a function of time.

In our numerical simulation, out of all factors that influence the growth of microorganisms only two were treated as variable. These are the amount of organic exudation by plant roots and the oxygen content of the soil solution. All other factors, including the nitrogen content, were assumed constant over the analyzed time interval. Two substrate sources are considered. One is the root system, releasing substrate into soil, and the other is soil itself, where the substrate is formed through decomposition of organic materials contained in soil (humus, fertilizer, and plant litter). The rhizosphere zone that we model is subject to active diffusion processes. The specific organic substrate present in root exudates both diffuses from the root surface into this zone and diffuses out of this zone. Oxygen also gets into the rhizosphere by diffusion and is utilized in respiration of rhizosphere microflora and plant roots. The content of mineral nitrogen is a model parameter and must be specified for each simulation variant.

The model is based on the following main assumptions. The first is that the rhizosphere microbial community is represented by just two populations—one is nitrogen fixers and the other is nonfixing microorganisms. This assumption is supported by the fact that microorganisms prevailing in the rhizosphere of different plants are largely determined by their functional capabilities rather than taxonomic affiliations. In addition, a given generic type of microorganisms can be characterized by assigning appropriate values (determined from experimental data) to model parameters that enter equations as constant factors. Also, there are several studies [7] in which complex microbial communities, including those in soil, were treated as a single population and its kinetic growth parameters were identified.

The second assumption is that the rhizosphere can be regarded as a reasonably homogeneous medium and described by a pointwise model. Indeed, in most studies [8], the radial extent of the rhizosphere zone is assumed to be of the order of 10 μm. The size of rhizosphere zones in our simulations was even smaller. In our model, the rhizosphere is represented by a set of narrow spatial regions bounded by concentric cylindrical surfaces with homogeneous conditions inside. The corresponding characteristics are allowed change only at boundaries between different zones.

The third assumption made in our model is that the migration of microorganisms into and out of the rhizosphere zone can be neglected. The nutrient content gradient, directed normally to the root surface, appears to preclude active migration out of the rhizosphere zone. As regards the inward migration, at the start of the succession (the first to third day of seed germination), the rhizosphere is dominated by bacteria that are *r*-strategists. Their growth rate is so high that the migrants penetrating the rhizosphere from the outer soil zones as a result of chemotaxis will hardly ever make up a significant part of the rhizocenosis.

The fourth important assumption is the absence in the equations of a term accounting for maintenance requirements of microorganisms. This term is believed to be a necessary complement to the Monod equation [9]. However, it was established in comprehensive investigations that maintenance requirements were not constant and, moreover, under a nutrient deficit, their variation had a clear-cut ecological significance [2]. Therefore, maintenance requirements are not a stable characteristic of a given bacterial strain and can fluctuate under the influence of numerous environmental factors. Based on literature evidence [2, 9], one can predict that neglecting the maintenance requirements in the proposed model will result in that the obtained growth curves of microorganisms will pass somewhat higher than the curves computed with maintenance requirements taken into account.

The first equation of equation set (1) describes the growth rate of a population of nitrogen-fixing bacteria. In the absence of migration from the rhizosphere zone, this rate is equal to the difference between the multiplication rate and the death rate of microorganisms. By supposing that the substrate is supplied to microorganisms via a transport system obeying the simple Michaelis–Menten kinetics, the specific multiplication rate μ can be expressed as

$$\mu = \mu_{\max}\left(\frac{S}{K_S + S}\right), \qquad (2)$$

where $\mu_{\max}$ is the maximum possible specific rate of multiplication; S is the substrate content; and K_S is the Monod constant, equal to the content of the limiting substrate at which the multiplication rate is half of its maximum value. The growth rate of a culture limited by nitrogen or oxygen is described by a function similar to (2).

In our model, the associative nitrogen-fixing microorganisms are allowed to switch the pathway of their metabolism by utilizing either molecular nitrogen from air or mineral nitrogen contained in soil and fertilizer [10]. It is postulated that, in soils rich in mineral nitrogen, diazotrophs tend to switch from the metabolic pathway of fixing molecular nitrogen from air to that

involving utilization of mineral nitrogen. Conversely, a shortage of mineral nitrogen causes nitrogen fixers to switch back to utilizing molecular nitrogen from air. The transition of bacterial cells from one state to another is, to some extent, a random process that maintains a steady balance between the numbers of microorganisms with different metabolic pathways of nitrogen utilization depending on the nitrogen content of soil. Meanwhile, a part of the microflora does not participate in nitrogen-fixation activities whatever the conditions but competes with both groups of dinitrogentrophs for the organic substrate and oxygen in the rhizosphere.

Mathematically, this is contention is equivalent to incorporating two different terms in the first equation of (1) to describe the growth dynamics nitrogen-fixing bacteria. The first term accounts for the number of nitrogen fixers that at the given moment utilize mineral nitrogen,

$$X_1\mu_{1N}\frac{SPN}{(K_{S1}+S)(K_{P1}+P)(K_{N1}+N)}, \quad (3)$$

where μ_{1N} is the maximum specific growth rate of nitrogen-fixing bacteria utilizing mineral nitrogen and K_{S1}, K_{P1}, and K_{N1} are the Monod constants for growth limited by the substrate, oxygen, and mineral nitrogen, respectively.

The second term describes the change in the number of nitrogen-fixing bacteria the metabolism of which at the given moment follows the pathway of atmospheric nitrogen fixation,

$$X_1\mu_{1F}\frac{SP}{(K_{S1}+S)(K_{P1}+P)(K_{N1}+N)}\frac{K_{PF}}{K_{PF}+P}, \quad (4)$$

where μ_{1F} is the maximum specific growth rate of nitrogen-fixing bacteria when fixing atmospheric nitrogen and K_{PF} is the Monod constant for growth limited by oxygen in associative nitrogen fixation. Under anaerobic conditions and under the conditions of high partial pressure of oxygen, the fixation of nitrogen by microaerophilic bacteria is known to be totally inhibited [11]. The factor

$$\frac{K_{PF}}{K_{PF}+P} \quad (5)$$

in (4) accounts for this dependence of nitrogen fixation upon partial oxygen content.

Therefore, with the cell death taken into account, the equation describing the growth dynamics of the nitrogen-fixing population will be given by

$$\frac{dX_1}{dt} = X_1\mu_{1N}\frac{SPN}{(K_{S1}+S)(K_{P1}+P)(K_{N1}+N)} + X_1\mu_{1F}\frac{SP}{(K_{S1}+S)(K_{P1}+P)(K_{N1}+N)}\frac{K_{PF}}{K_{PF}+P} - d_1. \quad (6)$$

The second equation in (1) relates to the whole diversity of soil microorganisms that lack the ability to fix nitrogen and are in direct competition with nitrogen fixers for the specific organic substrate released by the root system. By analogy with (6), the equation describing the growth dynamics of microflora competing with the population of nitrogen-fixing bacteria can be written as

$$\frac{dX_2}{dt} = X_2\mu_2\frac{SPN}{(K_{S2}+S)(K_{P2}+P)(K_{N2}+N)} - d_2. \quad (7)$$

The third model equation expresses the balance in the rhizosphere of dissolved carbon compounds. The first and second terms in this equation account for the consumption of organics in the rhizosphere by nitrogen fixers and their competitors and are given by

$$-\frac{X_1}{Y_1}\mu_1\frac{SP}{(K_{S1}+S)(K_{P1}+P)}, \quad (8)$$

$$-\frac{X_2}{Y_2}\mu_2\frac{SP}{(K_{S2}+S)(K_{P2}+P)}. \quad (9)$$

The explicit form of the other terms in this equation was derived using the following additional assumptions. The rhizosphere is supposed to be represented by a cylindrical soil layer bounded on the inside by the outer root surface of radius r and on the outside by a surface of radius R. Therefore, the model applies to the soil layer of size $(R - r)$. According to the first Fick's law, the net quantity of a substance crossing a section of unit area in unit time can be expressed as

$$F = -D\frac{dS}{dx}, \quad (10)$$

where F is the substance flux, $\frac{dS}{dx}$ is the substrate gradient in the direction of the X axis, and D is the diffusion constant. In models of the rhizosphere applied to very thin radial layers of soil adjacent to the root that are sufficiently uniform with respect to most of parameters [1], the net flux across the two surfaces (10) can be represented in a simplified form as

$$F = -2D\frac{S-S_0}{R-r}. \quad (11)$$

Then, the third term of the equation, describing the substrate diffusion outflow from the rhizosphere zone, can be written in the form

$$-D\frac{4R(S-S_0)}{(R-r)^2(R+r)}. \quad (12)$$

The substrate inflow to the rhizosphere depends on the root exudation value W and the level of background soil organics L available to microorganisms. Then, in expanded form, the equation that describes in (1) the

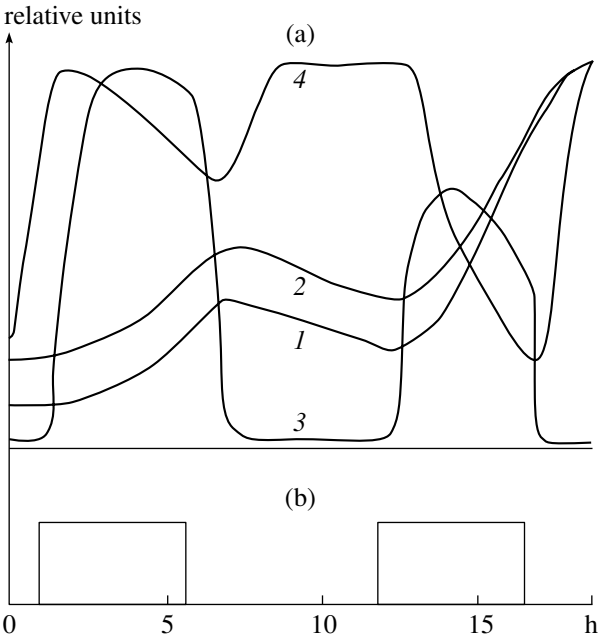

Fig. 1. (a) Solution curves for the system of four differential equations constituting the simulation model and (b) root exudation function: curve *1* shows the growth dynamics of nitrogen-fixing bacteria; curve *2* shows the growth dynamics of nonfixing microorganisms; curve *3* shows the variation of the organic substrate content; and curve *4* is the variation of the oxygen content.

variation of the substrate content of the rhizosphere can be written as follows

$$\frac{dS_1}{dt} = -\frac{X_1}{Y_1}\mu_1\frac{SP}{(K_{S1}+S)(K_{P1}+P)} - \frac{X_2}{Y_2}\mu_2\frac{SP}{(K_{S2}+S)(K_{P2}+P)} - \frac{2RD_S(S-S_0)}{(R-r)^2(R+r)} + \frac{2r}{R^2-r^2}W + L, \quad (13)$$

where Y_1 and Y_2 are, respectively, the yield coefficients for substrate utilization by the nitrogen-fixing bacteria and the competing microflora.

The fourth equation in (1) describes the rate of change of the partial pressure of oxygen in the rhizosphere. Because the amount of oxygen spent in soil microflora respiration is directly related to the amount of the specific organic substrate utilized by the nitrogen-fixing bacteria and by the competing microflora, we can simply divide the corresponding first two terms in equation (13) by the yield coefficients for oxygen utilization by the nitrogen-fixing bacteria Z_1 and the competing microorganisms Z_2. Taking into account that the oxygen diffusion flux is directed into the rhizosphere zone, we obtain

$$\frac{dP}{dt} = -Z_1\frac{X_1}{Y_1}\mu_1\frac{SP}{(K_{S1}+S)(K_{P1}+P)} - Z_2\frac{X_2}{Y_2}\mu_2\frac{SP}{(K_{S2}+S)(K_{P2}+P)} + \frac{2RD_P(P_0-P)}{(R-r)^2(R+r)} - L_P. \quad (14)$$

Equation set (1) was solved numerically using the Runge–Kutta method with a variable step.

In order to effectively apply this model in the dynamics analysis of specific populations, the model parameters characterizing microorganisms, plants, and soil had to be identified. The definitions and symbolic names of these parameters are given in the table, which also lists their approximate values estimated from literature sources. It should be noted that all these parameter values will not necessarily correspond to the actual conditions occurring in soil. Nevertheless, the reported figures are average values selected by thorough analysis of literature data and are suitable for theoretical predictions in terms of our model.

Microbiological parameters. The values of the microbiological parameters X, μ_{max}, R, Y, and Z were determined by several authors in experiments involving liquid aerated cultures and in soil conditions at temperatures ranging from 15 to 37°C [4, 12]. The value of μ_{max} for bacterial growth on readily utilized substrates was in the range 0.14–0.85 h^{-1}, depending on the medium composition and the particular microorganism. The yield coefficient Y for substrates readily utilizable by bacteria (such as glycerol, glucose, and lactate) did not show much variation and was equal to 0.41–0.45 g/g. The Michaelis constant K_S with respect to the substrate expressing the affinity of the microorganism to this substrate can vary broadly. In [12], the value of K_S for a mixed culture isolated from soil and growing on a liquid medium was estimated to be 45 μg C/g in carbon units. Two more values of K_S, equal to 2 and 10 μg/cm^3, are reported in [1]. The Michaelis constant K_P for growth limited by oxygen is much smaller than K_S and equal to 0.5 μg/cm^3 [13]. The death rate of cells in humid soil is taken to be 0.05 h^{-1} [4].

Parameters associated with plant activities. The data on the exudation rate of organic molecules are usually reported in literature for the whole plant and in most cases relate to seedlings [1, 3, 4]. However, to use our model for theoretical predictions, we have to know the exudation rates for different root segments. Since no experimental data of this kind could be found in the literature, we used, instead, the ratio of the mass of dry soluble organics contained in exudates to the root mass. It follows from our data that, for young 14-day-old plants of tomatoes, wheat, and ryegrass grown on arti-

Parameters and their reference values used in the mathematical model

Parameter	Definition	Unit	Reference value
	Microbiological parameters		
X_1	Biomass of nitrogen fixers	μg/cm^3	5.0
X_2	Biomass of competing microorganisms	μg/cm^3	10.0
μ_f	Maximum specific growth rate of the fixing part of nitrogen fixers	h^{-1}	0.8
μ_n	Maximum specific growth rate of the nonfixing part of nitrogen fixers	h^{-1}	0.5
μ_2	Maximum specific growth rate of the competing microorganisms	h^{-1}	0.5
K_{S1}	The Michaelis constant for nitrogen fixers with regard to substrate	μg/cm^3	5.0
K_{S1}	The Michaelis constant for the competing microorganisms with regard to substrate	μg/cm^3	10.0
K_{Pf}	The Michaelis constant for the fixing part of nitrogen fixers with regard to oxygen	μg/cm^3	0.1
K_{P1}	The Michaelis constant for the nonfixing part of nitrogen fixers with regard to oxygen	μg/cm^3	0.5
K_{P2}	The Michaelis constant for the competing microorganisms with regard to oxygen	μg/cm^3	0.5
Y_1	Yield or efficiency of substrate utilization by nitrogen fixers	μg/μg	0.4
Y_2	Yield for the competing microorganisms	μg/μg	0.6
Z_1	Efficiency of oxygen utilization by nitrogen fixers	μg/μg	0.8
Z_2	Efficiency of oxygen utilization by the competing microorganisms	μg/μg	0.8
	Plant-related parameters		
W	The root exudation function	μg/(cm^2 day)	50.0
S	Substrate content of the rhizosphere	μg/cm^3	variable
R	Soil zone radius	cm	0.03
r	Root radius	cm	0.02
	Soil parameters		
L_0	Initial substrate content	μg/cm^3	0.1
P_0	Initial oxygen content	μg/cm^3	5.0
N_0	Initial nitrogen content	μg/cm^3	5.0
D_S	Substrate diffusion constant	cm^2/h	0.0001
D_P	Oxygen diffusion constant	cm^2/h	0.0002

ficial liquid media, the root exudation can be estimated at 56.1, 28.6, and 0.34 μg organic matter per milligram of dry roots [14]. For roots grown in a solid medium, this estimate should be doubled. Consequently, when these plants grow in soil, over a 10-day period, they can exude from 0.6 to 110 mg organics/g dry roots. Assuming the specific weight of a young root to be roughly equal to 1.0 g/cm^3, its radius to be 0.02 cm, and the weight ratio of wet and dry roots to be 10, the rate of exudation from a unit cylindrical root surface will be in the range 0.6–110 μg/(cm^2 day).

Soil parameters. The diffusion constant for soil can be determined from the following relationship [1]:

$$D = \Phi D_S, \quad (15)$$

where D_S is the diffusion constant for root exudates in the solution and Φ is a coefficient dependent on the soil water content. In order to estimate Φ for various soils, the values of Φ for Cl ions were determined for different moisture levels from literature data [15]. It was found that, for a soil water content of 0.30 cm^3/cm^3, the coefficient Φ for Cl ions was equal to 0.20–0.25. This value can be immediately used in studies of the diffusion in soil of negatively charged organic acids contained in exudates. However, as shown in [15], the values of Φ for Cl ions and uncharged polyethylene glycol molecules are virtually equal. This suggests that uncharged organic molecules such as sugars have a coefficient Φ similar to that of Cl ions.

The values of D_S for diffusion of simple organic molecules in water can be found in many papers and

usually fall in the range $(0.5–1.0) \times 10^{-5}$ cm^2/s. Using (15), the diffusion constant D for molecules of root exudates in soil can be estimated at 1.0×10^{-6} cm^2/s. It follows that, in our model, the diffusion constant for soil with a water content of 0.30 cm^3/cm^3 can be set to 1.0×10^{-6} cm^2/s.

According to present-day estimates, one gram of cultivated soil might contain 10^8–10^9 bacterial cells [16]. A typical soil bacterium has a volume of 1 μm^3, a specific weight of 1.0 g/cm^3, and a wet-to-dry weight ratio of 10 [17]. It follows that the dry weight of 10^8–10^9 bacterial cells is 10 to 100 μg, and, in our model, the initial density of bacteria in soil could be set to 10 μg/cm^3. The average values of other soil parameters used in the model were also determined from literature data [15, 18].

The obtained numerical values of the parameters used in the model are very approximate and intended only as a starting point for model tests. Depending on the specific problem at hand, these values could be varied within fairly large limits. By doing so, the effect of inaccurate determination of the initial model parameters can be to a large degree cancelled. Based on the entire set of parameter values given in the table, reference values were set and used in computations.

Shown in Fig. 1a are graphs of the solutions of the four equations of set (1) obtained using the reference parameter values. The root exudation W was represented by a stepwise function (Fig. 1b) reflecting the exudation activity dynamics. The obtained graphs show that the concentration in the rhizosphere of the organic substrate was highest in the beginning of the first root exudation cycle (curve *3*). After completion of the first exudation cycle (6 h), a change in the dynamics of organic matter and bacterial biomass was observed. The content of organic substrate in the rhizosphere declined rapidly to its pool level in soil. At the same time, the biomass of both groups of microorganisms (curves *1* and *2*) decreased steadily because of growth limiting by the carbon source. The oxygen content (curve *4*) was generally lower than normal except for a short period when it reached its natural level in soil.

During the second root exudation cycle, the net biomass increased rapidly with faster growth shown by nitrogen-fixing microorganisms. The effect of insufficient mineral nitrogen content in the soil layer immediately adjacent to the root (10 μm), as determined by the initial parameter values, was quite significant. The oxygen content once again decreased to its minimum in the course of the second cycle. The organic substrate content was lower in the second cycle because of high accumulated biomass and the corresponding substrate utilization. In this period, the growth rate of microorganisms competing with nitrogen fixers was higher.

We see that the proposed model is able to quantitatively describe the variation of the number of associative nitrogen-fixing microorganisms in the plant rhizosphere as a function of the rate of carbon substrate exudation by roots. By varying the reference values of model parameters, the effect of different factors on the behavior of the two competing populations of rhizosphere microorganisms can be examined. Our model can be used to study the dynamics of separate groups of microorganisms in the rhizosphere by taking into account a fairly large number of factors of different nature (external factors; resources utilized—contents of soluble organic compounds, oxygen, and mineral nitrogen compounds; and biotic factors—the rate of root exudation and the competition between microorganisms).

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