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EXPERIMENTAL ARTICLES

Macrokinetics of Microbial Growth and Decline in Soil

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Abstract—Within the frameworks of the macrokinetic approach and continuum conception, a simple analytical model for the dynamics of microbial biomass (or derivatives of this value) in soil was developed. The model was tested against reliable published experimental data. The distinguishing feature of the model is its ability to describe the complete bell-shaped curve of microbial growth and decline in the absence of information on substrate availability.

Keywords: macrokinetics, population dynamics, growth curve, growth rate, decline rate, succession.

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Understanding the functioning of the soil microbial complexes requires studies of their dynamics [1]. The complete growth curves describing microbial growth in soil usually have the shape of a deformed bell. Without being supported with theoretical models, they are interpreted qualitatively or quantitatively using empirical and statistical models [1, 2]; this results in a decrease of the informativeness of the data. Thus, the models developed in terms of the biokinetic approach [3, 5] describe only the ascending slope of the microbial growth curve and not the phase of decline, this decreasing their usefulness in interpreting microbial growth in soil. Application of multiparameter models implies simultaneous measurements of the microbial growth dynamics, presence of available substrates, and parameters of the medium required by the particular model [5, 6]. To avoid the difficulties that arise in the organization of such experiments, it is effective to enhance informativeness of the easily recordable curves describing the dynamics of microbial activities in soil.

The aim of this study is to deduce an equation describing the indices of the activity dynamics of soil microorganisms as function of a variable—time.

MATERIALS AND METHODS

Deducing the Model

The model is deduced in terms of the macrokinetic approach [3] and continuum conception [4]. In our case, the continuum consists of cells and surrounding substrate components of the medium, where, assuming equilibrium conditions and constancy of pressure and temperature, chemical and biochemical reactions continuously take place, causing permanent synthesis and degradation of biomass; the rates of these reactions depend significantly on the mass-transfer processes. Notably, in any volume, however small, of the continuous environment, the concentrations of the primary elements participating in chemical and biochemical reactions are the same as their concentrations in the whole volume of the model continuum.

With the above assumptions, the complete system of differential equations describing the object cells plus medium is as follows [7]: $\frac{dq}{dt} = q\bar{F}(\vec{c})$, $\frac{dc_i}{dt} = qf_i(\vec{c})$ $i = 1, 2, ...$, where q is the biomass or an index derived from it; t is the time; $\vec{c}$ is the complete set of compound concentrations in the object; and $\bar{F}$ and f_i are the specific rates of growth and substrate utilization, respectively (calculated per unit of biomass or per number of cells). The solution of this system of equations is the vector $q(t)$, $\vec{c}\,(t) = q(t), c_1(t), c_2(t), ...$, which is a function of time. Substitution of $\vec{c}\,(t)$ into the equation $\frac{dq}{dt} = q\bar{F}(\vec{c})$ results in

$$\frac{dq}{dt} = q\bar{F}(\vec{c}(t)) = qF(t). \quad (1)$$

The task is to find an explicit solution of (1). The form of $\vec{c}\,(t)$ is known to be always complex [7] and to depend on the numerous parameters of the functions $\bar{F}(\vec{c})$, $f_i(\vec{c})$ and on the initial data for $q(t)$ and $\vec{c}\,(t)$, thus determining complexity of solution. Hence, the functions that describe the rates of microbial biomass

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Table 1. Macrokinetic characteristics of the dynamics of microbial biomass in soil

Specific point	Interval	q	q'	q''
t_0, of the beginning of growth	$t_0 < t \le t_1$	$+\uparrow$	$+\uparrow$	$+\uparrow$
t_1, of the greatest concavity to the left from the maximum	$t_1 < t \le t_2$	$+\uparrow$	$+\uparrow$	$+\downarrow$
t_2, of the bend to the left from the maximum	$t_2 < t \le t_3$	$+\uparrow$	$+\downarrow$	$-\downarrow$
t_3, of the greatest convexity to the left from the maximum	$t_3 < t \le t_4$	$+\uparrow$	$+\downarrow$	$-\uparrow$
t_4, of the maximum	$t_4 < t \le t_5$	$+\downarrow$	$-\downarrow$	$-\uparrow$
t_5, of the bend to the right from the maximum	$t_5 < t \le t_6$	$+\downarrow$	$-\uparrow$	$+\uparrow$
t_6, of the greatest concavity to the right from the maximum	$t_6 < t$	$+\downarrow$	$-\uparrow$	$+\downarrow$

Notes: q, biomass or a value derivative from it; q', rate of biomass alteration; q'', acceleration; "+", function is positive; "−", function is negative; ↑, function increases; ↓, function decreases.

increase (first to the right) and decrease (second to the right) are formulated as

$$qF(t) = q\frac{K}{t^2} - q\frac{b}{t}, \quad (2)$$

so that the integral of their sum will correspond to the experimental data, which are frequently [1] described by a deformed bell curve. K here is the coefficient of microbial biomass increase rate, and b is the coefficient of microbial biomass decrease rate.

Substitution of (2) into (1) results in

$$\frac{dq}{dt} = q\left(\frac{K}{t^2} - \frac{b}{t}\right). \quad (3)$$

The solution of (3) is

$$q = \frac{C}{t^b}\exp\left(-\frac{K}{t}\right), \quad (4)$$

where C is the constant of integrating with the meaning of a coefficient scaling q value.

Coefficients C, b, and K Eq. (4) can be calculated using experimental data by the methods of nonlinear regression implicated in available applied computer programs, in our case [8]. The algorithm of any such programs implies introduction of approximate values of the unknown coefficients. These approximate values were calculated by using the following equations:

$$\ln C = \frac{c_3a_1b_2 - c_3b_1a_2 - c_1a_3b_2 - c_2a_1b_3 + c_2b_1a_3 + c_1a_2b_3}{b_2a_1 - b_1a_2 - a_3b_2 - b_3a_1 + b_1a_3 + a_2b_3}, \quad (5)$$

$$b = \frac{c_2a_1 - c_1a_2 + (a_2 - a_1)\ln C}{b_2a_1 - b_1a_2}, \quad (6)$$

$$K = \frac{c_1 - bb_1 - \ln C}{a_1}, \quad (7)$$

These formulations were deduced by the Gauss methods [9]. Here, $a_i = -1/t_i$, $b_i = -\ln t_i$, and $c_i = \ln q_i$, where q_i is the current microbial biomass at the moment t_i. Substitution of q_i and t_i into (5)–(7) in three points of the whole experimental body yields approximate values for the coefficients of Eq. (4). As model (4) describes growth from the very beginning at t_0, which is not known exactly, an amendment to the measured growth value was introduced: instead of the argument t, an expression $t + \tau$ was used, where τ is an additional parameter.

Study of the Model

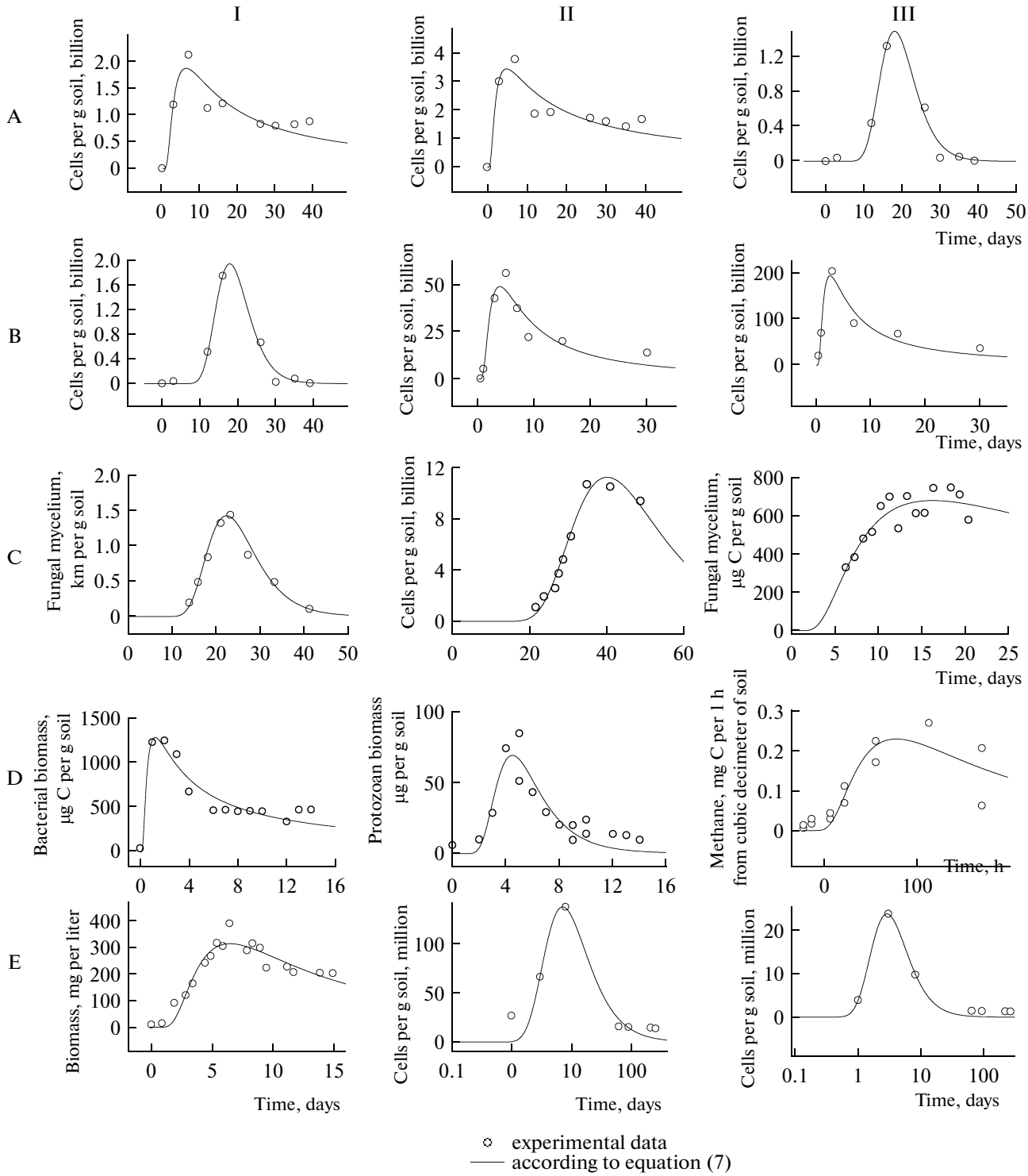
After substitution of (4) into (3) we obtain

$$\frac{dq}{dt} = \left(\frac{K}{t^2} - \frac{b}{t}\right)\frac{C}{t^b}\exp\left(-\frac{K}{t}\right).$$

The analysis of this equation shows that, if $t = 0$, its right part does not exist, and if $t \longrightarrow 0$, then it does exist, but $q \longrightarrow 0$. Thus, the conclusions drawn on the basis of the model do not contradict the common biological concepts.

Let us consider three cases of application of Eq. (4). In the hypothetical case in which biomass growth is absent and $K = 0$, the equation graph is hyperbolic. In the artificial case, when $b \longrightarrow 0$, the Eq. (4) graph is an S-shaped curve (similar to the curves for logistic functions) aiming at the limiting value determined by the integration constant C. In the most common case, in which all the constants differ from zero, the Eq. (4) graph is a deformed bell curve with a maximum at a certain moment of time (Fig. 1). To find the special points of this graph, the derivatives of the first, second, and third orders of (4) with respect to time were analyzed at fixed constants. Six special points were revealed that separated intervals with individual macrokinetic characteristics (Table 1). For the maximum,

$$t_4 = t_{\max} = \frac{K}{b}. \quad (8)$$



Verification of Eq. (7): A I, dynamics of the total number of bacteria in chernozem after initiation of succession by wetting [10, Fig. 1-1]; A II, the same after wetting and glucose addition [10, Fig. 1-2]; A III, dynamics of the total number of viable gram-negative bacteria during microbial succession in chernozem in the control [10, Fig. 4-1]; B I, the same after addition of glucose [10, Fig. 4-2]; B II and B III, dynamics of the population of *Pseudomonas denitrificans* in chernozem at a low and high initial number [2, Fig. 5]; C I and C II, dynamics of the growth of fungi and bacteria in chernozem after addition of glucose [3, Fig. 57]; C III, D I, and D II, dynamics of the growth of fungi, bacteria, and protozoa in gray forest soil after addition of glucose [3, Fig. 56]; D III, dynamics of the growth of methanogens in peat [11]; E I, dynamics of the growth of *Penicillium funiculosum*, dominating the amylolytic community of podzolic soil, after addition of starch and glucose [3, Fig. 29]; E II and E III, dynamics of root nodule bacteria in soddy–podzolic soil [2, Fig. 15] with and without introduction of hydrolytic actinomycetes.

Table 2. Coefficients of model (4) (in the first column are the numbers of the objects from the figure caption)

no	C	b	K	t_{max}	q_{max}	τ
A I	51.2	1.2	7.4	6.3	1.9	0.0
A II	32.8	0.9	4.2	4.9	3.4	0.0
A III	8.44×10^{49}	27.5	654.2	23.8	1.5	5.8
B I	8.44×10^{49}	27.8	626.2	22.5	1.9	4.7
B II	2199.9	1.6	6.3	3.9	48.8	0.0
B III	3120.9	1.4	3.7	2.6	194.7	0.0
C I	2.11×10^{49}	26.2	726.0	27.7	1.4	5.2
C II	2.11×10^{49}	22.5	1153.4	51.2	11.4	10.7
C III	72095.6	1.2	20.0	16.2	678.3	0.0
D I	5259.5	1.1	1.5	1.4	1274.7	0.0
D II	1.41×10^{49}	32.8	335.0	10.2	67.5	4.1
D III	44756.9	2.3	184.9	82.1	0.2	0.0
E I	159271.2	2.2	14.2	6.5	312.9	0.0
E II	8568.9	1.4	9.9301	7.1	138.1	0.0
E III	2371.5	2.3	6.4	2.8	23.8	0.0

RESULTS AND DISCUSSION

The working hypothesis regarding the adequacy of describing the experimental data on the dynamics of microbial growth in soil by Eq. (4) was accepted with a probability of 0.95 on the basis of regression analysis carried out by using the software package [8]. The hypothesis of the normality of distribution of experimental values relative to the values calculated and the hypothesis of their dispersion uniformity and the independence of residues were confirmed by assessment with the use of the criteria of Kolmogorov–Smirnov, Spearman, and Durbin–Watson, respectively. Theoretical curves describe realistically the published experimental data [2, 3, 10, 11] (Fig. 1), which represent major types of bell-shaped curves (symmetrical, asymmetrical, pointed, flat, and gently and steeply sloping) and the commonly accepted methods for their measurement. When microbial growth is described kinetically with the use of Eq. (1), the time control function is formulated [3] in such a way that integral (1) corresponds to the experimental data. In our case Eq. (2) describing the process rate leads to Eq. (4) describing the dynamics of microbial biomass in soil. When coefficients are fixed (Table 2), this equation results in a deformed bell-curve, which is characteristic of the dynamics of intermediate products of chemical reactions. This distinguishes it from the equations resulting in *S*-shaped curves striving to a certain positive limit (these curves are characteristic of the dynamics of the final product). Equation (4) describes complete dynamics of microbial biomass (or of derivative values) in soil, from the beginning of growth until its end. Calculation and analysis of the derivatives from Eq. (4) with respect to time allows the boundaries for intervals with equal kinetic characteristics to be precisely determined. Equation (4) constants can be calculated on the basis of data on the dynamics of microbial biomass in soil or any related parameter of microbial activity by the least squares method with the use of available software packages. At the same time, Eq. (4) constants with the graph including any three experimental points can be calculated using the Eqs. (5)–(7).

Thus, in terms of the macrokinetic approach and continuum conception, a model describing the dynamics of microbial biomass in soil was developed. This model allows the researcher to analyze the experimental curves describing the activities of soil microorganisms in time in the absence of data regarding substrate. In all of the investigated cases, this model behaves realistically.

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