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Understanding and prediction of soil microbial community dynamics under global change

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Abstract

The review deals with quantitative descriptions of soil microbial processes in northern terrestrial ecosystems and predictions of their possible modifications under anticipated global changes. The main focus is the dependence of population dynamics of soil microorganisms on environmental factors. To simulate microbial dynamics, mechanistic mathematical models are suggested which summarize the contemporary information on physiology and molecular biology of organisms representing different life strategies. The major independent environmental factors were clustered into three main groups: (i) soil mineral resources (available and deposited biogenic elements); (ii) factors related to solar radiation (sunlight, clouds, temperature, active layer, UVB); and (iii) factors affecting gas and liquid mass transfer (soil texture and porosity, vascular transfer, water regime). The quality and amount of organic matter which provide the sources of C and energy for most soil microorganisms are considered as dependent variables and can be generated by simulation models as a product of biosynthetic activity of plants and microorganisms. A strong interaction between different factors has been demonstrated, e.g. temperature and amount of available C nutrients which can be explained in physiological terms. The simulation of the tundra microbial community revealed its relatively high stability to global warming. Elevated temperatures and input of dead organic matter relieved the pressure of L-selection and accelerated an aerobic decomposition of dead organic matter (plant litter, soil humus).
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Keywords: Soil microorganisms; Population dynamics; C balance; Mathematical simulations; Greenhouse gases; Environmental factors

1. Introduction

Understanding succession mechanisms and describing soil community dynamics under fluctuating environments has been traditionally one of the most important and challenging problems in soil ecology. In the last decade, the Global Change agenda has given new stimulus to this topic. However, soil micro-

bial community research remains well behind the mainstream of the Global Change studies. The primary efforts have been directed at the effects of anticipated changes in climate and environment (elevated CO₂ in air, N deposition, warming, etc.) on higher organisms – plants and animals, including both, experimental studies and mathematical simulation of population dynamics at different time scales (Fantechi et al., 1991). Few relevant works have been specially devoted to soil biota, microorganisms and microfauna. This gap is critical in view of the impor-

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tance of the ecological functions of microbial communities which carry out unique processes vital for the whole ecosystem: decay of plant litter, nitrogen fixation, denitrification and nitrification, formation and consumption of trace gases, transformation of metals, sulfate reduction, production of phytohormones, etc.

The main aim of the paper is to address the problem of quantitative description, understanding and mathematical simulation of soil microbial dynamics which can be translated into ecosystem level impacts. Microorganisms are considered to be much more reactive components as compared with plants and animals. Although the old view, namely bacteria multiply in natural environments at the same rate as in nutrient broth (the generation time down to 20 min), was shown to be completely erroneous, nevertheless some favorable soil microsites (rhizosphere, animal gut, feces, etc.) do provide rather rapid bacterial growth, equivalent to 1–2 generations per day, while other less beneficial microsites permit no more than one generation per 3–10 days during the summer season (Brock, 1971; Panikov, 1995). Global climatic changes operate on much longer time scales, from a decade to centuries, with slow shifts in yearly mean values of temperature/precipitation and other parameters. As seasonal fluctuations are much greater, the direct effects of climatic changes on microorganisms should not be significant. Much more essential must be the indirect effects caused by shifts in plant community structure, quantity and quality of plant litter, supply of nutrients, modification in the physical and chemical characteristics of the environment due to soil erosion, nutrient leaching, flooding, etc. Therefore, to make a realistic prediction on the fate of microbial communities under global change and to elucidate the microbially mediated mechanisms of such change, we have to take a holistic view of the entire terrestrial ecosystem including the plant community and animals as well as the physical and chemical environment.

The review reflects the state-of-the-art of mathematical modeling in microbial ecology. It is focused on northern terrestrial ecosystems because

1. they contribute strongly to the C budget of the whole biosphere (deposition and decay of dead organic matter);
2. they play an important role in production and consumption of CO₂, CH₄ and other greenhouse gases;
3. it is here that climate change is predicted to be the greatest; and
4. the northern ecosystems, e.g. tundra, are relatively simple.

More specifically, we will try to answer the following questions.

- What are the principal driving forces controlling the dynamics of soil microbial communities?
- What minimal information on community structure and environmental parameters is needed for a successful simulation and prediction?
- What is the relationship between biodiversity and ecological functioning of the soil microbial community?

A systems approach is used to address these and similar questions, based on combinations of laboratory experiments, field observations and mathematical modeling. The mathematical model plays a very important role in testing various hypotheses, discarding the obviously wrong ones (which do not agree with experimental data), and simulating ecosystem responses to changing environments according to different scenarios.

2. General assessment of available mathematical models

The models describing microbial growth and activity can be deterministic and stochastic, empirical and mechanistic, numeric and analytic, dynamic and static, etc. Many models deal with isolated microbial populations or even single cells, describing the effects of environmental factors. This review concentrates only on mechanistic, deterministic and dynamic models, dealing with entire soil ecosystems containing plants as primary producers, microorganisms using organic substrates as a source of C and energy, and soil microfauna which interact with plant and microbial populations by grazing microbial mass, phytomass or plant litter, stimulating microbial activity in the gut and excrement, etc.

There are recent reviews of models describing primary productivity and decomposition in terrestrial ecosystems (McGill, 1996; Smith et al., 1996; Paustian, 1994). Some models, like CENTURY (Parton, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, USA) are intensively used in applied ecology to predict the effects of land use, pollution, climatic changes in particular ecosystems. Input parameters are weather data, soil characteristics, plant growth and land management parameters. Model outputs are soil temperature, water, carbon and nitrogen dynamics, as well as the rates of phytomass, decomposition of organic matter, nitrification–denitrification, etc. These *process-oriented* models (Paustian, 1994) focus on the processes of movement and transformation of matter or energy and do not account for organisms (microorganisms, animals, plants) as explicit state variables. The microbial biomass is sometimes treated as an active pool of soil organic matter (OM) (Jenkinson, 1990; Parton et al., 1988), but the real mechanisms of microbial activity, including cell multiplication and growth, induction and repression of degrading enzymes, co-metabolism of lignin and humus are not expressed. Instead, decomposition of OM is represented as a ‘self-decay’ of several ($n=1$ to 4) arbitrary groups of OM, e.g. readily decomposable and stable plant litter components, humus, etc.:

$$\frac{ds}{dt} = -k_1s_1 - k_2s_2 \cdots - k_ns_n \equiv - \sum_{i=1}^n k_i s_i \quad (1)$$

where s_i is the residual content of OM in the i th fraction, and k_i the respective first-order rate constant.

The effects of environmental parameters (temperature, moisture, pH, soil texture) on the rate constant are expressed via various semi-empirical functions. For example, the dependence of the soil respiration rate on temperature (T) and soil moisture content (θ) is described by the equation representing the net physiological responses of different organisms (Flanagan et al., 1993):

$$R(\theta, T) = \frac{\theta}{a_1 + \theta} \frac{a_2}{a_2 + \theta} a_3 a_4^{(T-10)/10} \quad (2)$$

where a_1 – a_4 are empirical parameters.

The obvious advantage of process-oriented models is their relative simplicity which allows simulation at

larger spatial and temporal scales. However, as these models do not express explicitly biological mechanisms, they lack the required generality and may fail to simulate the observed biodynamics without significant site-specific calibration.

One step forward to tackle biological mechanisms is provided by the so-called *organism-oriented models* which simulate the flows of matter or energy through different functional or taxonomic groups of soil organisms (Paustian, 1994). These groups can be very general (e.g. bacteria, fungi) or represent more specifically developed detrital food webs (Hunt et al., 1987). The next step is to formulate such mathematical equations which represent the real biological mechanisms known from contemporary physiological and molecular studies. The main problem to be resolved here is how to avoid either an oversimplification or excessive intricacy while keeping such models manageable. A compromise lies in the concept of coordinated microbial biosynthesis, represented in the *synthetic chemostat model - SCM* (Panikov, 1991; Panikov, 1996), stemming from an idea put forward by Powell (1967). Independently, chemical approaches led to construction of *cybernetic growth models* having similar (but not identical) mathematical structure (Turner et al., 1989).

Microbial growth is described by SCM as conversion of limiting substrate(s) into new cell mass via low-molecular weight intermediates. The composition of de-novo synthesized cell material is allowed to vary in response to environmental factors (contrary to other models which assume the constancy of cell composition and physiological properties). Thus, SCM simulates adaptive ‘purposeful’ behavior of microorganisms which should be considered as the main distinctive feature of organisms as compared with chemical catalysts or isolated enzymes. As a result, these models provide efficient research tools for examination of complex dynamic behavior of microorganisms: growth and survival, differentiation and extinction, steady-state and transient dynamics, variations in cell composition, synthesis of by-products, etc.

3. Diversity of soil organisms and environmental factors

One of the most essential features of any natural soil ecosystems is the greater complexity and diversity of

biotic and environmental components as compared with artificial systems. This feature presents the main obstacle to constructing realistic mathematical simulations.

3.1. *Microbial biodiversity*

Most of the known mathematical simulations deal with the total amount of microorganisms which carry out specific biogeochemical functions. In reality, any particular physiological group of microorganisms (methanogens, methanotrophs, nitrifying bacteria, heterotrophic aerobic microorganisms, etc.) is represented by a number of populations competing for common substrates. The difference between various populations of the same trophic niche is related to their life strategy (Gerson and Chet, 1981; Panikov, 1995).

We can distinguish three types of life strategies which have evolved under the pressure of three different environmental circumstances occurring in natural selection: r-selection (pioneer stages of succession, the state of temporary ecological 'vacuum'), K-selection (climax stages at the most intensive competition), and L-selection (in adverse environments). Numerous field observations in combination with laboratory studies allow us to identify particular organisms as predominantly r-, K- or L-selected and to find specific physiological features responsible for their competitive advantage under different environmental conditions. K-selected organisms (synonyms: autochthonous and oligotrophic bacteria and fungi) develop high affinity to monomeric substrates, low maintenance requirements, the ability to uncouple growth from transport and respiration under transient growth conditions, to accumulate rapidly deficient C-substrate as reserve polymeric compounds, etc. The r-selected organisms (synonyms: copiotrophic and zymogenic populations, 'sugar fungi') are characterized by intensive growth and have excessive biosynthetic machinery under growth limitation (ribosomes, enzymes of primary metabolic reactions) which secure their instant growth response under temporary relief from starvation. L-selected organisms can be of two types. One group is adapted to unfavorable environment (psychro-, thermo-, halo-, acido- and alkalotolerant organisms). The second group has adapted to starvation stress by formation of dormant structures (spores, cysts), production of

antibiotics and extracellular enzymes degrading unfavorable 'second-rate' substrates (aromatic and polymeric compounds).

To describe the behavior of soil microorganisms with different life strategies, we can use the new generation of kinetic models like SCM. Each strategic type is described by an individual model reflecting currently available data on physiology and molecular biology of particular microbial species (Panikov, 1996). The laboratory experiments with pure and mixed cultures of individual organisms are the only source of information on their metabolic responses to environment. To extrapolate laboratory ex situ data to natural in situ situations, the main option is to test in laboratory culture a wide range of growth conditions (temperature, substrate concentration, spectrum of assimilated substrates, dynamic pattern of substrate delivery). Then, as a measure of congruence, one may use integral characteristics (e.g. specific growth rate) of the given population. If these values overlap for ex situ and in situ populations, then the laboratory model may be regarded as relevant and may be used for prediction.

3.2. *Diversity of environmental factors*

There are numerous factors affecting soil microbes, as well as plant roots and animals (Fig. 1). It is not realistic to simulate all these factors because such a mathematical model would be too complicated and awkward for subsequent analysis, testing and practical use. Besides, the number of potentially significant factors shows the tendency to increase as we learn more and more about the system. Fortunately, we can considerably reduce their number by taking into account the following considerations:

- a limited number of factors are really *primary independent variables* and should be viewed as input parameters of simulation models. Others are *secondary dependent variables* which can be 'automatically' generated by mathematical models based on known mechanistic relationships;
- all known factors/variables can be assembled into several categories of functional types, each category representing common mechanisms involved in environmental control of microbial activity;
- the number of essential factors can be further reduced for specified conditions and ecosystems

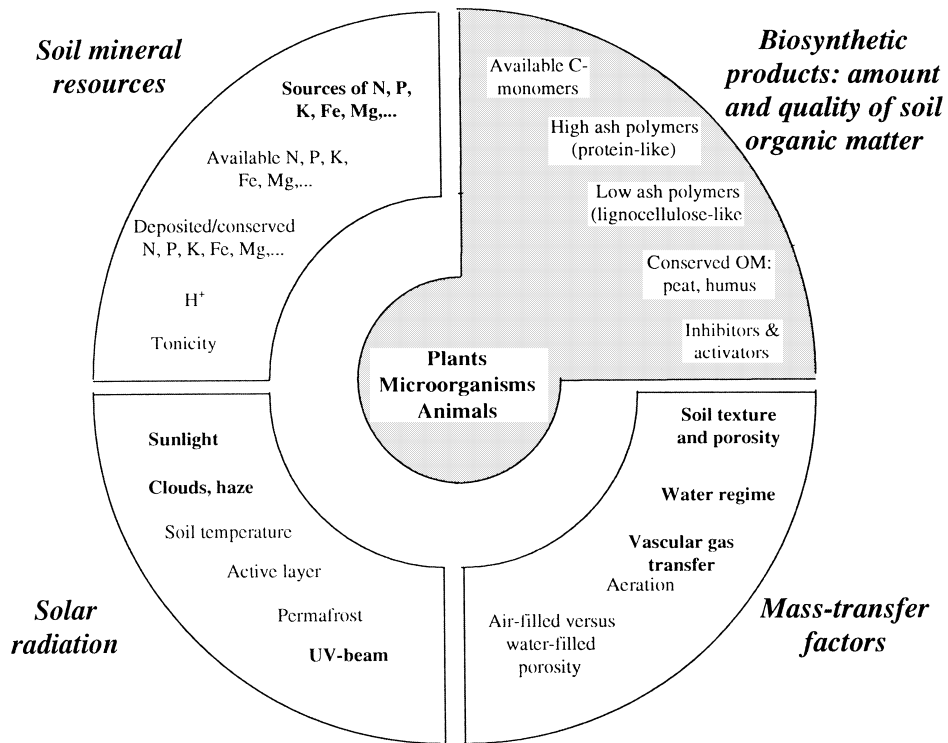


Fig. 1. Environmental factors affecting soil communities including the primary independent (bold letters) and dependent variables (plain letters). For further explanation see text.

after identifying the most critical and fundamental processes and organisms.

Applying these principles to analysis of soil organisms (i.e. organisms utilizing dead organic matter), we may conclude that there are only three groups of truly independent environmental factors (Fig. 1).

1. The soil mineral resources which include sources of mineral macro- and micronutrients for plants and microorganisms derived from soil, subsoil (underlying rock material), run off and atmospheric deposition. The effects of mineral nutrition is strongest in respect of plants, although in some oligotrophic ecosystems (e.g. in ombrotrophic bogs) even heterotrophic soil organisms can be limited by availability of N, P, K and other mineral compounds. Only some part of mineral nutrients is immediately available, the rest being immobilized in various forms (located in live active, resting or dead cells, insoluble, adsorbed,

chelated, etc.). As a rule conversion into available form is catalyzed by soil organisms, say, due to the action of hydrolytic enzymes or production of chelating exometabolites like siderophores. Mathematical simulations accounting for the effects of mineral resources are based on the set of differential equations, describing all known sources and sinks for each particular element or chemical species in question. Frequently, we may accept quasi-steady state approximation and use equilibrium constants (dissociation, complex formation, oxidation–reduction, etc.) available from the models of classical chemistry.

2. Sunlight and radiant heat determine most of the ecosystem's energy balance, seasonal variation of soil and air temperature, and depth of active layer to permafrost. The primary variables are solar radiation and physical state of the atmosphere (e.g. clouds and aerosol density, greenhouse gases), the other variables, including soil temperature profile and active layer depth, are generated by

the atmospheric radiative transfer model supplemented with the soil's physics module (Stammes et al., 1988). The UV-component of sunlight can also affect soil organisms, both directly (by modifying biosynthesis of light-exposed organisms, mainly plants) and indirectly (through change in plant litter quality).

3. The soil solid phase controls the rates of gas and liquid mass-transfer which determine variation in patterns of ecosystem functioning between such extremes as wetland (low exchange rates, stagnant water regime, formation of anaerobic soil layers due to low O₂ transfer rate) and dry sandy soils characterized by a strictly aerobic and water-deficient regime due to intensive aeration and high hydraulic conductivity. Soil moisture may not be necessarily critical per se as a source of water; much more frequently it is the volume of water-filled pores which affects the activity of soil biota through the limitation of gas transfer including O₂ flux from the atmosphere. The gas channel in waterlogged soil can also be provided by roots of some plant. The simulation of soil moisture and heat fluxes is based mainly on the use of differential equations in partial derivatives and is a well-developed instrument in applied soil physics (Philip and de Vries, 1957; Marshall and Holmes, 1988).

In contrast to inorganic compounds, soil organic matter (OM) should be considered as a dependent variable in the models simulating ecosystem dynamics. The reason is obvious: most OM is the product of instant biosynthetic activity of plants and microorganisms which are the biotic components of a given ecosystem. The only exception is allochthonous substances (airborne or delivered with run off), but their contribution to the total C balance of soils is low. There are various ways to characterize soil OM in terms of susceptibility to degradation. The simplest way is to use apparent half-decay time $t_{0.5}$ of any individual compound or fraction of soil OM: $t_{0.5} = \ln 2/k$, where k is the first-order rate constant in Eq. (1). It implies that decomposition of different OM occurs as (i) a simple first-order decay reaction similar to that of radioactive isotopes, (ii) independently of other OM fractions (absence of priming effects or repression), and (iii) simultaneously for easily decomposable and

recalcitrant compounds. In reality, OM decomposition involves principally different mechanisms: multiplication and growth of responsive microorganisms, induction and repression of degrading enzymes, co-metabolism of lignin and humus, physical dispersion of plant litter by soil animals, etc. Therefore, it is advisable (Panikov, 1995) to differentiate soil OM into the following five categories (Fig. 1):

1. Available C-monomers derived from root exudates and enzymatic breakdown of macromolecules. These low molecular weight substances need not be transformed outside the cells before consumption, e.g. monosaccharides, amino acids, nucleosides and other aliphatic and aromatic compounds which are 'normal' low molecular weight intermediates of primary cell metabolism.
2. The macromolecular chemical species with balanced element composition, i.e. having high contribution of 'ash' elements, namely P, N, CA, or proteins, nucleic acids, lipo- and glycoproteides. These macromolecular compounds are easily available for microbial degradation because they contain major growth elements. Normally, they are degraded by extracellular enzymes (proteases, nucleases, phosphohydrolases, etc.) which are reversibly repressed by monomers of group 1.
3. The structural insoluble and 'low-ash' macromolecular C-compounds of unbalanced composition (lignocellulose, hemicellulose, pectin). Their degradation is considerably impeded by a deficiency of N, P and other biogenic elements needed for microbial synthesis. That is why their decomposition is slow and requires involvement of entire communities of interacting microorganisms with different functional capabilities to cope with such OM (producers of hydrolytic enzymes and siderophores, N₂-fixing bacteria, mycelial organisms importing deficient nutrients from outside decomposition loci, etc.). Apart from catabolic repression of degradation enzymes, saprotrophic organisms deprived of N and P under excess of C-substrates can enter the state of severe metabolic inhibition which was termed 'substrate accelerated death' (Panikov, 1995). The relief from this suppression is provided by cycles of freezing-thawing, drying-rewetting and passing through intestines of soil invertebrates. The relationship among saprotrophic

microorganisms and invertebrates in the soil may rarely be competitive; in most situations these interactions are through positive cooperation during decomposition of OM, as well as ‘prey–predator’ or ‘host–parasite’ interactions.

4. Conserved OM (humus, sapropel, oil, resins, waxes, etc.) are those end products of metabolic or abiotic physical/chemical reactions which acquire resistance to degradation or further transformation. They are completely excluded from intensive transformation. Some conserved organic materials are potentially available for decomposition, e.g. peat within permafrost or anaerobic horizons. Under the effects of considerable perturbation (permafrost thaw, drainage of wetland, fertilization, etc.) peat undergoes a rather quick degradation.
5. The inhibitors and activators are specific metabolites produced by soil organisms and play the same role as hormones in the development of plants and animal bodies. The data on these compounds are very limited and available mainly for model systems (Kaprelyants et al., 1993).

3.3. Interactions between different environmental factors

Different soil factors overlap and interact with each other in their effects on soil organisms. Moreover the organisms themselves can provide feedback to the environmental factors. There are many familiar examples of interactions between factors like moisture–aeration and permafrost–soil texture relationships. Less familiar are the feedbacks between organisms and environments, e.g. effect of medium acidity on microbial activity feedback from microorganisms to soil pH because of uptake and excretion of strong anions and cations. We will illustrate interaction and feedback phenomena in relation to temperature which plays an especially important role for northern ecosystems.

The effects of temperature depends very much on the nutritional status of the environment. Fig. 2 demonstrates our unpublished data on the temperature dependence of soil respiration, measured in amended, and unamended, soil samples. In a temperate bog, addition of glucose strongly accelerated respiration at

low but not at elevated temperatures. The tundra soil displayed the opposite type of response: glucose amendment stimulated respiration at higher temperatures, whereas under cold conditions stimulation was moderate. Thus, we see that temperature responses depend on other environmental factors, e.g. the content of available C-substrate, and this dependence may be different for soils having different past-histories. To interpret these data in sound physiological terms, we have examined the long-term response of microorganisms to added substrate by following their growth at different temperatures. One way to record growth dynamics is to measure the soil respiration rate $v(t)$ which is related to microbial biomass $x(t)$ as follows (Panikov and Sizova, 1996):

$$v(t) = [W(t) + Q]t \quad (3)$$

where t is the time, Q the metabolic quotient which is constant under non-inhibitory excess of oxidizable substrate, and W the respiratory activity uncoupled from growth due to maintenance (osmoregulation, protein turnover, cell motility) and energy-spilling reactions protecting cell from surplus of catabolites (Tempest and Neijssel, 1984).

Fig. 3 presents an example of respiration dynamics measured in amended soil samples at different temperatures. The relative contribution of productive and wasteful respiration to the total rate can be derived from the shape of dynamic curves because only productive respiration is responsible for observed exponential growth of $v(t)$. If $W(t)$ is high, then we see the distinct lag-phase indicating adaptive changes in microbial community before start of growth. At the other extreme (W is negligible as compared with Q) the exponential growth takes place immediately without a lag-phase. As can be seen from Fig. 3, the lag-phase at low temperature occurred only in the temperate soil while in the tundra soil growth was exponential (although rather slow) even at 1°C. Wasteful respiration at zero time was minimal in tundra soil at low temperatures and in temperate soil at a mesophilic temperature range around 20°C (Fig. 3(C)). The reason for high non-productive respiration under cold incubation conditions is self-heating of cells in a temperate soil (a well-known phenomenon for higher organisms) when the oxidation energy is completely dissipated as heat. The increase of non-pro-

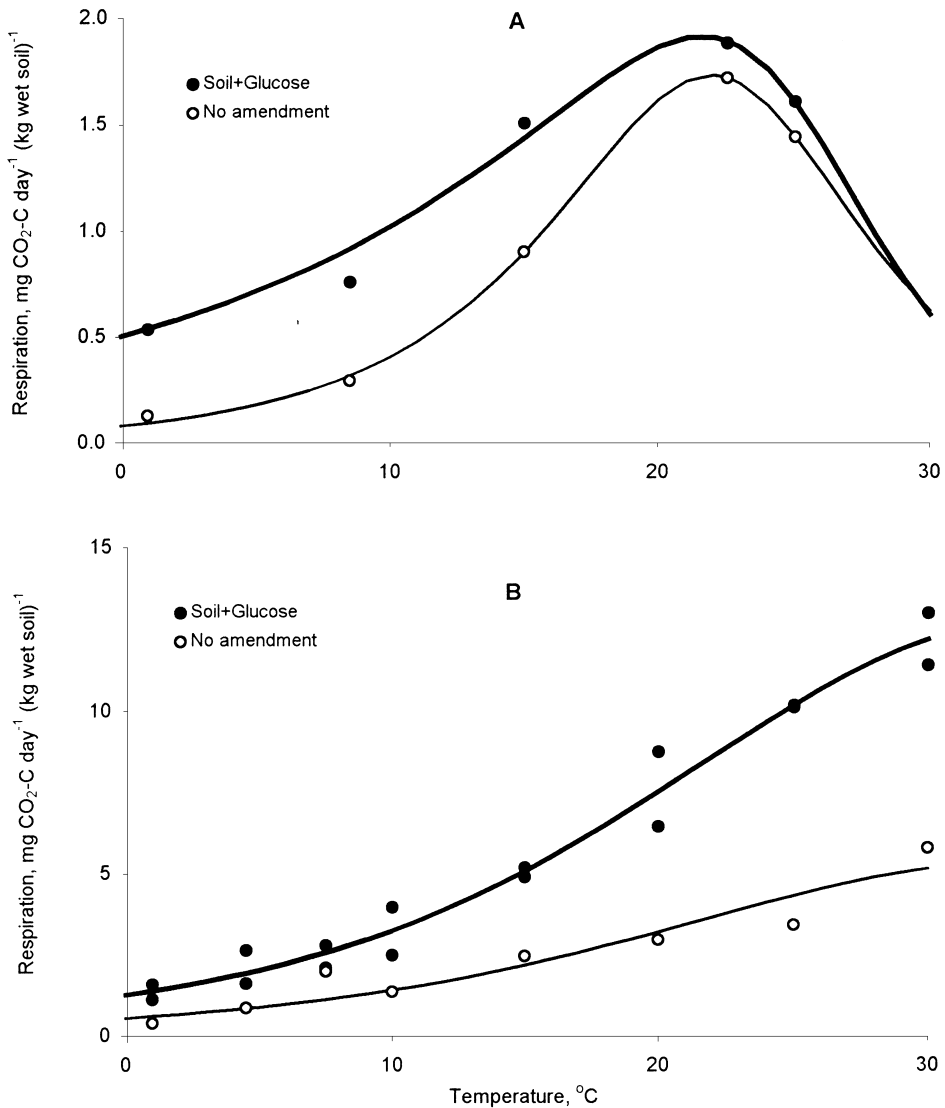


Fig. 2. The effects of temperature on respiration rate of two soils in relation to glucose addition. A: temperate soil, ombrotrophic *Sphagnum* peat bog under dwarf pine forest (Tomsk Area, West Siberia, 56°53'N, 82°50'E), pH(H₂O) 3.2, organic layer 5–10 cm. B: Tundra soil, subzone of subarctic, polygon tundra (Tareya, Taymyr Peninsula, 73°15'N, 90°36'E); the sampling site was located on polygons under *Carex*, *Salix* and mosses, pH(H₂O) 4.9, organic layer 2.5–5 cm. Experimental setup: 10 g of moist soil was mixed with water or glucose–mineral mixture containing (per 1 g soil): 5 mg glucose, 1 mg KH₂PO₄, 1 mg (NH₄)₂SO₄. The respiration rate was recorded by IR-gas analyzer Infralit4 (Germany), air flow rate 500 ml/min. (Panikov and Sizova, unpublished data). Note that the difference in absolute values of respiration rates between the two soils are mainly attributed to differences in soil density and water content. The curves were calculated according to the equation: $v=A \exp (aTC) / \{1+\exp [b(1-Q/T)]\}$, where v is the respiration rate, T the absolute temperature, TC the Celsius temperature and A, a, b and Q the kinetic constants.

ductive respiration in tundra soil at high incubation temperatures also indicates the non-optimality of growth conditions and the need for physiological adaptation.

Thus, kinetic analysis based on combinations of mathematical modeling and dynamic experiments can provide insights into underlying mechanisms and highlight the prospects for further experiments.

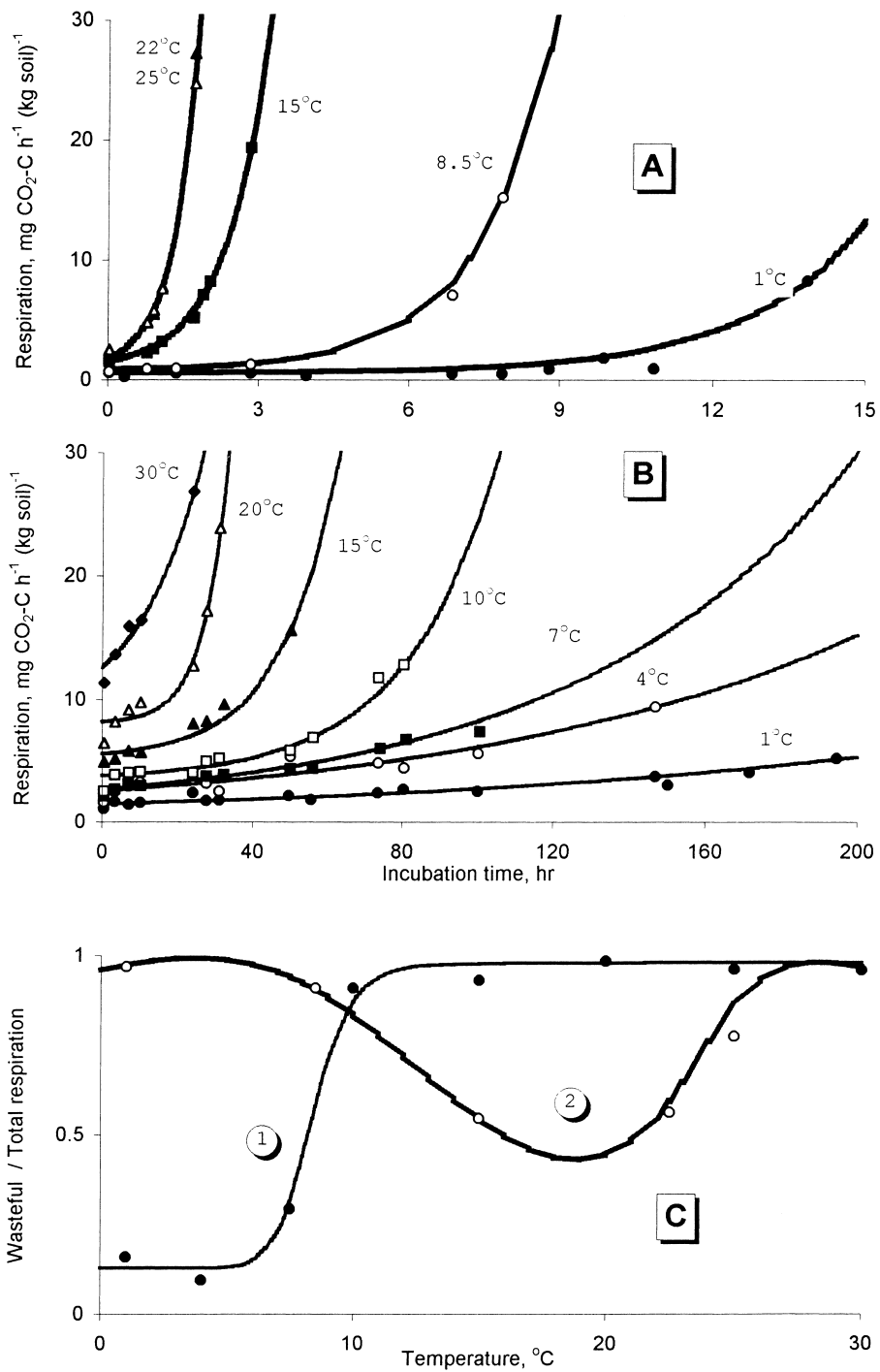


Fig. 3. The long-term effects of temperature on microbial growth in glucose-amended soils (see Fig. 2. for soil descriptions). (A) Temperate soil; soil respiration dynamics at various temperatures after glucose addition. (B) Tundra soil; soil respiration dynamics at various temperatures after addition of glucose. (C) The effects on the relative contribution of wasteful respiration to the total respiration of the soil community. 1, tundra soil and 2, temperate soil. For experimental conditions and soil description see Fig. 2. The curves were calculated from SCM (Panikov, 1995).

4. Simulation of tundra community dynamics under global warming

The rationale outlined above has been used to simulate the microbial population dynamics in arctic tundra at Point Barrow, Alaska and the anticipated response to global warming (Panikov, 1994). The simulation model was based on SCM. The microbial community was represented by three typical heterotrophic organisms (*Arthrobacter*, *Bacillus* and *Pseudomonas*) competing for one common organic substrate. *Arthrobacter* and *Pseudomonas* are, in fact, the most abundant bacteria in many tundra soil (Parinkina, 1989). However, these names are used in wider context representing the three strategic groups rather than the respective singular genera. Thus, the *Arthrobacter*-type organisms include not only the principally dominant *A. globiformis* but also other less abundant K-selected species like *Rhodococcus* and prostekate bacteria, fungi such as *Mortierella ramanniana*, etc. The *Pseudomonas*-type includes as the principal component *P. fluorescens* and other opportunistic species like *Achromobacter*, yeasts and ‘sugar’ fungi. The L-strategist *Bacillus* producing two subpopulations (vegetative cells and spores) was also assumed to produce hydrolytic enzymes initiating the breakdown of plant litter. This function is normally performed by other spore-forming organisms of this strategic group which are mainly fungi.

The annual temperature dynamics of Barrow was taken as the average over the period 1930–1960 (French, 1974). The elimination of microbial cells was assumed to be caused by protozoa, their grazing activity being suspended if prey biomass declined below some threshold level. Nutrient substrates for microbial growth were provided by the plant community, the gross primary production GPP being a direct function of temperature. The input of organic matter to soil was assumed to be via (i) root exudation (40% of GPP) and (ii) plant litter formation (60% of GPP). Root exudates consist of readily available compounds, while plant litter is composed of stable macromolecular compounds (pectin, lignocellulose, resins, etc.) which need prior degradation by hydrolytic enzymes. The average size of primary production, $260 \text{ g C m}^{-2} \text{ y}^{-1}$, as well as dependence of GPP on temperature, were taken from Tiezen (1974). The rates of plant litter decomposition and average litter

reserves (1500 g C m^{-2}) were assessed from the data of Flanagan and Veum (1974). The parameters of the microbial populations were identified from completely independent data on batch and continuous growth of *A. globiformis*, *P. fluorescens* and *B. subtilis* (Panikov, 1995).

The simulated present-day seasonal dynamics at Barrow under normally cold conditions (Fig. 4, the first two years) was characterized by the following features:

1. The microbial community was dominated by *Arthrobacter* and *Pseudomonas*, while bacilli displayed only sporadic short-term activation during spring.
2. The dynamics of *Arthrobacter* were stable throughout the year.
3. The *Pseudomonas* population varied within a wide range attaining peaks in late spring and autumn.

These results were fully supported by experimental data for arctic tundra in North America and Russia (Nelson and Visser, 1978; Parinkina, 1989) which report the spring and autumn peaks of bacterial abundance and sporadic detection of bacilli only at spring-thaw time. It should be noted that we did not introduce any special temperature requirements for these bacteria. Their competitive exclusion from arctic soils was brought about by one factor – the amount of available C-substrate. Sensitivity analysis revealed that only exceptionally strong eutrophication ($\text{GPP} > 5000 \text{ g/m}^2$) led to a greater abundance of *Bacillus* than other species. This accords with empirical observations that bacilli are abundant in very rich and highly productive soils (alluvial, meadow, chernozem, and manured soils).

The anticipated climate warming was simulated by rise of air temperature by 2° , 5° and 10°C throughout all seasons. Surprisingly, the resulting changes in the community structure were modest even at the maximum temperature shift of 10°C . There was some increase in the biomass of *Arthrobacter*, a slight decrease of the average *Pseudomonas* populations under the pressure of predation, and (most significant) an acceleration of *Bacillus* growth, i.e. their spring bursts became higher by one order of magnitude although remaining an order of magnitude less than the other groups (Fig. 4).

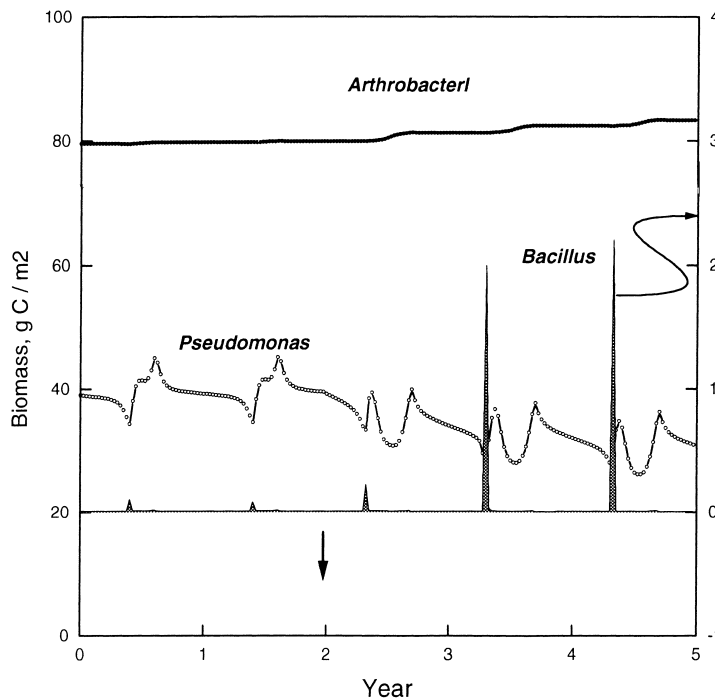


Fig. 4. Simulated soil biota responses to elevated temperatures: dynamics of bacterial biomass (Panikov, 1994). The arrow indicates a change in the climatic and environmental conditions with an increase in January temperature from -24° to -14°C , the number of frost-free days from 81 to 135, and the index of degree-days from 293 to 1365.

The main effect of rising temperature on the carbon balance of the ecosystem was a considerable activation of organic matter decomposition due to higher production of hydrolytic enzymes by L-strategists (Fig. 5). The primary productivity was also increased, but to a lower degree. As a result, the reserves of plant litter dramatically decreased (15% over the first year). A new steady-state value of plant litter was attained after 20–30 years (not shown) at a level of ca. 740 g C/m^2 or 50% of the initial values.

Separate simulations were used to follow the competition between psychrophilic and mesophilic subpopulations of *Pseudomonas* (Fig. 6). The first subpopulation absolutely dominated the bacterial community under cold conditions, and an increase in temperature by 5°C did not affect their domination. Further warming by another 5°C resulted in a rapid 50% substitution of psychrophiles by mesophiles over two years. Under the new quasi-steady state, the two subpopulations demonstrated a stable coexistence due to the regular seasonal changes of temperature, i.e. the first maximum in spring was due to the rapid growth of

psychrophiles, while the second autumn one was attributed to the mesophiles.

Thus, simulations displayed a high degree of stability of the microbial community with respect to the anticipated warming of climate. Significant changes in the functional structure took place only after a large increase in temperature, i.e. 10°C . Activation of *Bacillus* growth may be interpreted as a relief from the pressure of L-selection, the main factors being an increase in substrate availability due to self-accelerated hydrolytic/mineralization activity and elevated primary production.

How important is it to account for microbial biodiversity when simulating C-transformation in tundra soil? To answer this question, we performed a sensitivity analysis of the model. It turned out that reduction of microbial community by exclusion of at least one component (r-, K- and L-strategists or protozoa) led to a complete failure of the simulation: removal of protozoa introduced abnormal build-up of microbial biomass, the absence of L-strategists resulted in a decay of disappearance of hydrolytic activity, while the coex-

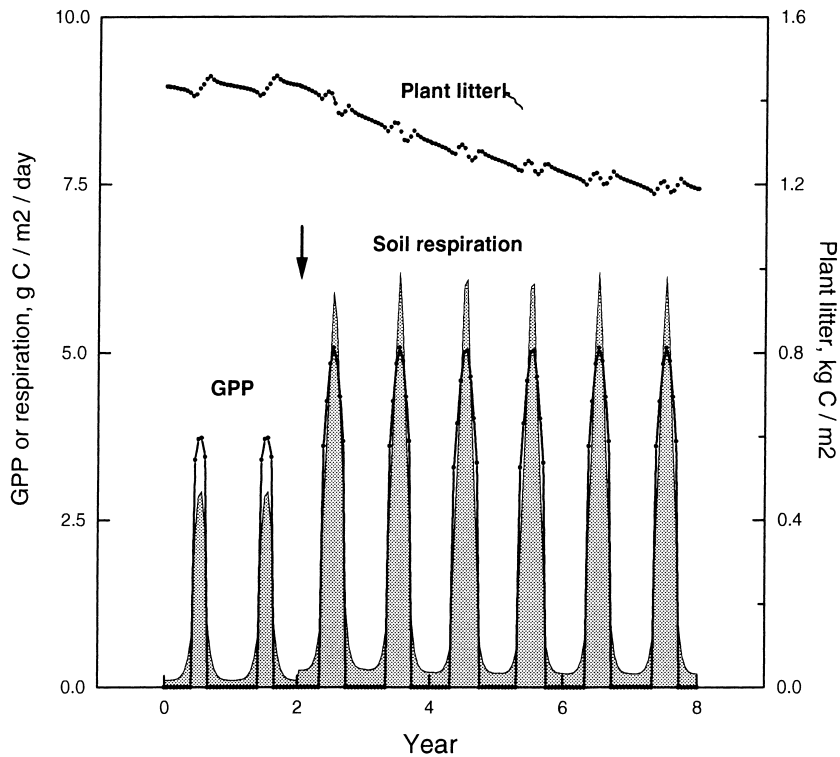


Fig. 5. Simulated response of a tundra ecosystem (Point Barrow, Alaska) to elevated temperatures: the dynamics of the main sources and sinks of organic carbon (Panikov, 1994). Changes in climate as in Fig. 4.

istence of r- and K-strategists was essential to secure rapid microbial growth in spring–summer transition.

5. Effects of soil moisture

Various climatic scenarios indicate that global warming might be associated with dramatic changes in soil water regime including both, soil flooding and temporary drying, as well as a general destabilization of the water regime. So far as tundra is concerned, reduction in microbial activity due to drought is unlikely or limited to some category of upland soils of light texture. Anyway, the direct instant effects of water deficiency is accounted for by models like Eq. (2). On the other hand, long-term effects of alteration in water regime is associated with aerobic–anaerobic transition and might cause dramatic changes in the composition of the microbial community. The establishment of anaerobic conditions because of decrease of mass-transfer of O_2 to submerged soil

layers initiates new microbial processes – denitrification, sulfate reduction, acetogenesis and methane formation, the latter being important for the radiative balance of the globe.

Most of the models describing methane emission are based on empirical relationships between CH_4 fluxes and environmental parameters, such as temperature and moisture/water table level (Roulet et al., 1992; Harriss et al., 1993; Frolkin and Crill, 1994). Although these factors are important, they are not sufficient, in themselves, to explain wide flux variations in time and space, as shown by the following arguments.

- Existing soil climate models do simulate dynamics of gas emission from particular wetlands but only after extensive site-specific calibration.
- Wetlands of the same type, e.g. *Sphagnum* peat bogs under similar climatic conditions, can vary in terms of CH_4 emission ($mg/day/m^2$) by several orders of magnitude, from -10 to $+30$ in the

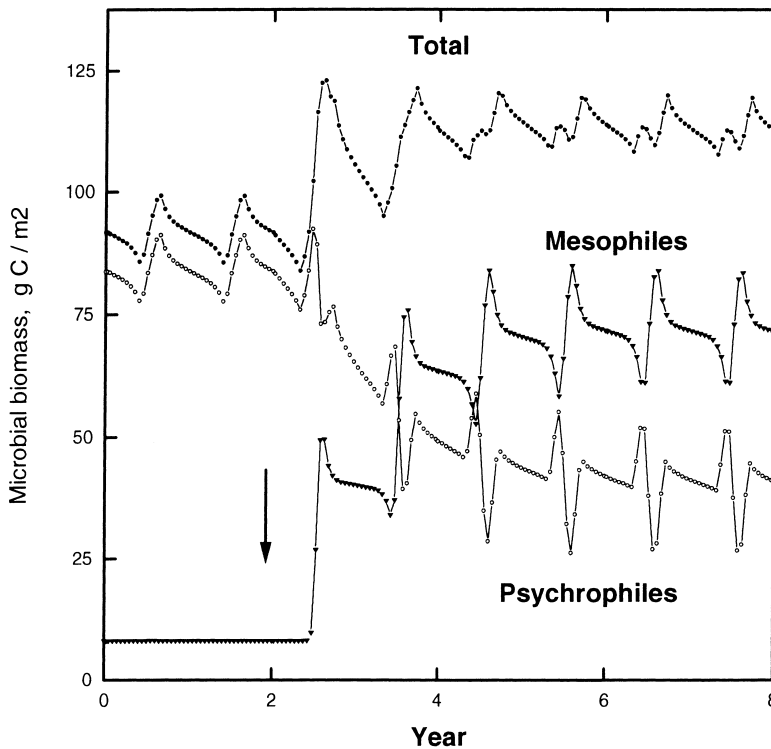


Fig. 6. Simulation of competition between psychrophilic and mesophilic subpopulations of *Pseudomonas* in tundra soil after rise in temperature. Changes in climate as in Fig. 4.

Hudson Bay, to 100–400 in the Vasyugan Lowland, West Siberia (Harriss et al., 1993; Panikov et al., 1995).

- Emission rates are generally correlated with temperature and moisture when data are analyzed for a single site with respect to time. However, this correlation rapidly declines for pooled data on fluxes measured at different geographical locations (Panikov et al., 1995).
- It is widely accepted that methane is emitted from anaerobic systems. However, anoxia (absence of O_2) is not the only condition required for intensive methane emission and methanogenesis may be suppressed by competing anaerobic processes (e.g. sulfate reduction and acetogenesis).

Thus, in addition to empirical relationships, more mechanistic considerations are needed to account for spatial and temporal variation in gas fluxes. The mechanistic models of methanogenic communities are discussed mainly in relation to waste-water treat-

ment rather than to natural terrestrial ecosystems (Buffiere et al., 1995; Westerman, 1994; Stams, 1994). The biochemistry of anaerobic digestion (Fig. 7) can be described schematically by major steps: breakdown of plant litter macromolecules, fermentation, acetogenesis and methanogenesis. These anaerobic metabolic networks are very sensitive to concentrations of intermediary products (H_2 , formate, acetate). Their accumulation above some threshold level inhibits activity of syntrophic bacteria. Inhibition is explained by the fact that VFA (volatile fatty acids) oxidation is thermodynamically only feasible at low hydrogen and formate concentrations, as is evident from a calculation of Gibbs' energy for any acetogenic reaction, e.g. in case of propionate oxidation:

$$\Delta G' = (\Delta H^0 - \Delta S^0 \times T) + RT \ln \left(\frac{[\text{acetate}] \times [\text{HCO}_3^-] \times [\text{H}^+] \times [\text{H}_2]^3}{[\text{propionate}]} \right) \quad (4)$$

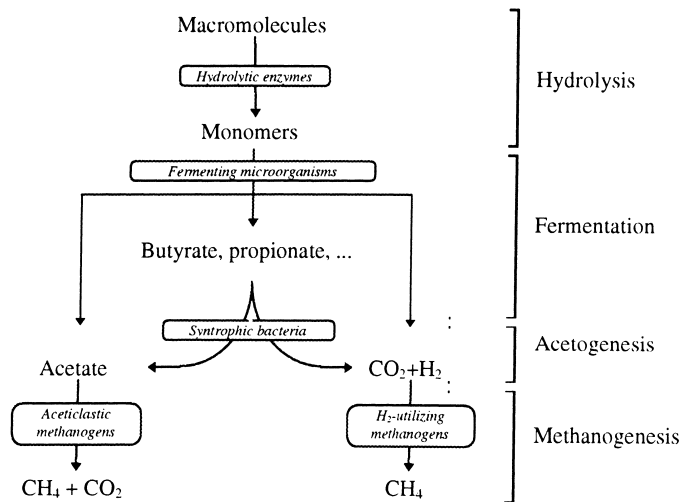
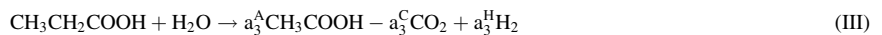
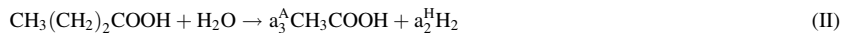
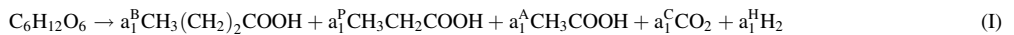


Fig. 7. Anaerobic transformation of organic matter to methane according to the following reaction stoichiometry:



^b -butyrate, ^P -propionate, ^A -acetate, ^C -CO₂, ^H -H₂

where ΔH^0 and ΔS^0 are the standard enthalpy and entropy of reaction, T the absolute temperature, R the gas constant, and values in square brackets are respective concentrations. At room temperature, $\Delta G'$ -value is negative (reaction is allowed) only if H₂ partial pressure is $<10^{-4}$ atm.

The biochemical and thermodynamic data on methanogenic communities await translation into ecosystem level impacts. There have been few attempts to proceed in this direction. The model of CH₄ emission, given by Cao et al. (1995), accounts for the carbon mass flow to the methanogenic community from primary products (plants) via the decomposition loop and rhizodeposition. This productive idea was also applied to model CH₄ emission on a global scale (Christensen et al., 1996). It was assumed that methane emission is proportional to heterotrophic respiration and net primary production (NPP) of waterlogged soils. Applied on a 1°-grid basis using standard climatological and wetland distribution data sets, this approach provides simulation of seasonal dynamics and a circumpolar estimate of total CH₄ emission.

The most advanced process-based one-dimensional model was developed by Walter et al. (1996). It describes explicitly the formation of methanogenic substrate via decomposition of plant litter and rhizodeposition as well as the main gas-transfer mechanisms including diffusion, ebullition and vascular transport. As a result, it provided almost perfect simulation of three-year observations on methane emission dynamics from a Michigan peatland.

Nevertheless, one of the most essential missing points is an account of the entire plant-microbe-animal system and internal multiple interactions within metabolic network (see Fig. 7) which are so important for anaerobic communities. The construction of these types of models is now one of the most urgent tasks in contemporary soil ecology.

6. Conclusions

This communication does not cover all aspects of mathematical simulation of microbial population

dynamics. The main message to be conveyed is that mechanistic mathematical simulations are practical useful tools for a better understanding of microbial life and function in the soil. The realistic simulation of seasonal and annual population dynamics of soil microorganisms is quite achievable, although it may require the use of rather complicated structured models. Let us summarize the main results to answer those questions which were raised in Section 1.

First of all, the principal driving forces controlling the dynamics of heterotrophic soil microorganisms should be identified as substrate flux (input of available C) and elimination of growing cells by predators. That is why a simulation of microbial dynamics needs to deal with entire ecosystems including primary producers (plants) and consumers (protozoa and other predators). To go further into underlying mechanisms of microbial decomposition of OM, we have to distinguish organisms containing and lacking hydrolytic activity, the first group being more vulnerable to severe growth limitation and starvation. Finally, it would be realistic to acknowledge the differentiation of non-hydrolytic organisms into rapidly and slowly growing ones, each of which have their own competitive advantage under changing environments. The designated components of microbial communities were assigned to three types of life strategies to emphasize the idea a continuum: there are no single r-, K- or L-strategists, instead all individual populations occupy the entire space within a common rKL-continuum.

The concept of life strategy provides a compromise which allows us to avoid both, over-simplification of the soil community (neglecting the biodiversity of organisms and biological control of litter decomposition) and overburdening the mathematical model with a large array of state variables. The simpler unstructured models which reduce a whole community to one integral variable 'microbial biomass' would inevitably lead to assumptions of 'self-decay' of OM (Eq. (1)) which does not agree with reality, although it can be used for formal description of decomposition dynamics.

The minimal model of soil microbial community described above is still applicable only to some relatively simple cases. We have indicated the ways to achieve further progress by incorporation of other state variables (additional groups of organisms, and

environmental factors clustering into three functional types) as well as biotic interactions other than simple competition for a common substrate: production of antibiotics, toxins and phytohormones, competition and positive cooperation between mycelial and single-cell organisms, symbiotic and parasitic relationships.

Concerning the issues of Global Change, we have to stress the necessity to test mathematical simulation against observation data. The lack of reliable methods to assess the biomass of the total community and particular functional groups remains the main obstacle to realizing such tests. Probably modern DNA-techniques will be especially useful for this purpose in future. Concerning the final modeling step, it is most desirable to construct a microbial submodel which is part of a master ecosystem model describing the parallel evolution of plant and microbial communities as well as soil physical and chemical properties rather than separate and independent models of microbial population dynamics.

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