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EXPERIMENTAL ARTICLES

Regulation of the Biomass and Activity of Soil Microorganisms by Microfauna

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Abstract—Microcosm experiments showed that the microbial biomass and the respiration activity in soil were regulated by nematodes. Depending on nematode number and plant residue composition, the trophic activity of nematodes can either stimulate or inhibit microbial growth and respiration as compared to soil containing no nematodes. The stimulating effect was observed when nitrogen-free (starch) or low-nitrogen (wheat straw, C : N = 87) organic substrates were applied. Inhibition occurred when a substrate rich in nitrogen (alfalfa meal, C : N = 28) was decomposed and the nematode population exceeded the naturally occurring level. A conceptual model was developed to describe trophic regulation by microfauna (nematodes) of the microbial productivity and respiration activity and decomposition of not readily decomposable organic matter in soil. The stimulating and inhibiting influence of microfauna on soil microorganisms was not a linear function of the rate of microbial consumption by nematodes. These effects are largely associated with the induced change in the physiological state of microorganisms rather than with the mobilization of biogenic elements from the decomposed microbial biomass.

Key words: microbial biomass, respiration rate, microfauna, nematodes, catabolic diversity

The regulating role of animals in the activities of the soil microbial community is related to the essential trophic role of microorganisms that serve for soil animals as a source of indispensable amino acids, vitamins, and phosphorus [1]. Unlike large invertebrates (earthworms, millipedes, and wood lice), which act upon soil as a habitat of all soil organisms [2], the invertebrates grazing on microorganisms (protozoa, nematodes, and microarthropods) directly affect microbial populations [3, 4]. It is believed that, to carry out their regulatory function, the biomass of animals needs to amount to 1–10% of the microbial biomass [5].

There is now ample evidence that the rate of processes carried out by soil microorganisms is to a large degree determined by soil animals [4]. The concentration of the forms of nutrient elements available to plants, the mineralization rate of not readily degradable substrates, and the plant production were shown to increase in the presence of fauna [6], and it was established that the respiration rate and growth of microorganisms in decomposing leaf litter and soil are affected by invertebrates [7–9]. There exist two different approaches in explaining these facts. According to the first one, the microbial complex is activated by invertebrates, which consume a part of the microbial biomass and liberate the nutrient elements bound in the biomass [6]. The other explanation assumes that invertebrates may affect the physiological state of soil microorganisms by mechanisms analogous to those involved in compensatory growth [10]. So far, there is no experimental proof of the operation of such mechanisms in soil.

The goal of this work was to study the functional importance of nutrient element mobilization by microfauna and of the change in the physiological state of microorganisms caused by microfauna in the process of plant residue decomposition in soil.

MATERIALS AND METHODS

Soil. Samples of soddy–podzolic soil under wood spruce forest (Moscow oblast) were taken from the humified A_1 horizon (carbon content, 1.2%; total nitrogen according to Kjeldahl, 0.09%; pH H_2O 4.6; N-NH_4^+-N, 7.2 mg/kg soil; and N-NO_3^-, 5.8 mg/kg soil). Prior to assays, the soil was cleared from roots and sieved; the mesh size was 5 mm. Samples of soil were stored under natural moisture conditions at a temperature of 12°C.

Enumeration of nematodes and microarthropods. Nematodes were extracted by the method of Baermann; microarthropods, by the method of Tullgren [9]. Counting of nematodes (stylet and non-stylet), col-

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lembolans, and mites in extracts was done under a light microscope.

Determination of the fungal and total microbial biomass. The total microbial biomass in tests with straw was determined by a modified fumigation-extraction method, in which samples of soil with natural water content are used for fumigation and the value of the k_c factor equal to 0.33 is adopted, as previously suggested for estimations of the microbial biomass in soils receiving additional organic matter [12]. In tests with starch and alfalfa meal, the total biomass and the fungal biomass were determined by the method of substrate-induced respiration [13] with bacterial growth suppressed with streptomycin.

Determination of the soil respiration activity. The respiration rate was estimated in terms of the rate of CO_2 emission from soil. Samples of soil with a dry weight of 5 g were dispensed into penicillin bottles, sealed, and incubated for 1 day at 23°C. Carbon dioxide was determined on a LKhM-80 gas chromatograph equipped with a thermal conductivity detector and a 2.7-m column filled with Polysorb-1; the thermostat temperature was 40°C; the carrier gas (helium) flow rate was 35 ml/min; and the sample volume was 0.5 cm^3.

Determination of the catabolic diversity of the microbial community. The catabolic diversity was estimated using a physiological approach [14] by measuring the change in the respiration rate of microorganisms caused by application of different classes of substrates: carbohydrates (glucose, galactose, or arabinose), amino acids (alanine or glutamic acid), organic acids (sodium citrate), and glycerol.

Determination of the mineral forms of nitrogen. Concentrations of NO_3^--N and NH_4^+-N were determined using ion-selective electrodes in water extracts (with a soil : water ratio of 1 : 2.5) for nitrate ions and in a 0.05 N Na_2SO_4 extract (with a soil : salt solution ratio of 1 : 2.5) for ammonium ions.

The laboratory microcosm method. Samples of native or defaunated soil (90 g) were dispensed into glass bottles (150 ml) with the addition of 1% ground wheat straw (C : N = 87), alfalfa meal (C : N = 28), or starch (no nitrogen). Microcosms were incubated in the dark at 23°C for 18 to 30 days. At regular intervals equal to 3 to 7 days, one bottle of each test variant was withdrawn for assays. In several experiments, the defaunated soil was refaunated with a complex of soil nematodes or microarthropods with a natural composition and numbers or a complex of nematodes with a doubled population size.

In order to compare the effects of microfauna and mineral nitrogen on the microbial complex activities, the initially defaunated soil was defaunated again after 14 days of incubation in humid state. Wheat straw was added to defaunated soil samples. On the 10th day of incubation, a natural complex of nematodes (about 200 individuals/10 g) or potassium nitrate was added in concentrations of 0.35, 0.78, 2.72, or 5.75 mg/g. The doses of nitrogen were calculated to obtain C : N ratios in the straw test variants equal to 80, 35, 10, and 6, respectively. The controls were represented by a defaunated variant without the addition of KNO_3.

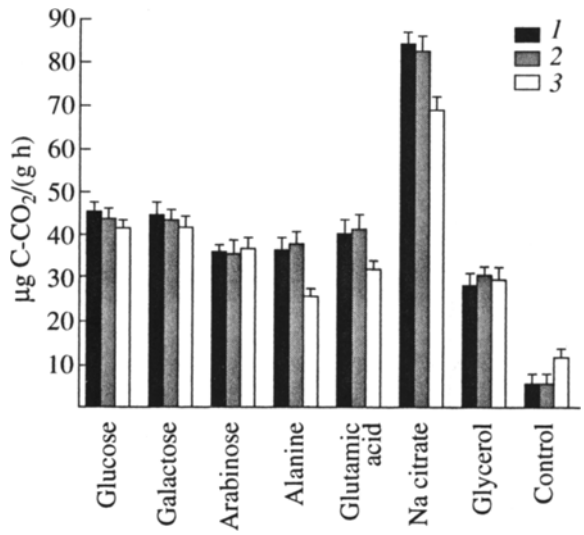

Fig. 1. Respiratory response induced by different substrates in (*1*) native and (*2*) defaunated soil and in (*3*) soil dried at 40°C for 1 day.

All experiments were performed in two replicates. All assays were replicated three or five times. The value of the standard deviation was estimated.

RESULTS

Soil defaunation method. When a researcher faces the task of assessing the influence of microfauna on the community of soil microorganisms, it is important that the effect of defaunation on the microbial complex be kept to a minimum. In order to study the influence of microfauna on the microbial biomass and the respiration rate, we had to modify the method previously described [15]. In the original method, soil was heated at 70°C for 3 h, which was observed to lead to a significant decrease in respiration activity. The modification we introduced was that a layer of native soil (2–2.5 cm) was covered with a wet filter paper and warmed at 55°C for 5 h without any significant loss of soil moisture (no more than 7% of the original value). The proposed technique quite effectively eliminated active live forms of soil nematodes and microarthropods without affecting the microbiological properties of soil: the content of microbial biomass (965 ± 51 and 1000 ± 47 μg C/g in native and defaunated soil, respectively), the respiration rate (41.5 ± 3.7 and 52.1 ± 4.2 μg CO_2-C/(g day)), and the concentration of water-soluble organic matter (171 ± 34 and 183 ± 42 μg C/g, respectively). The respiration rates in the native and defaunated soil measured over a period of 11 days after treatment turned

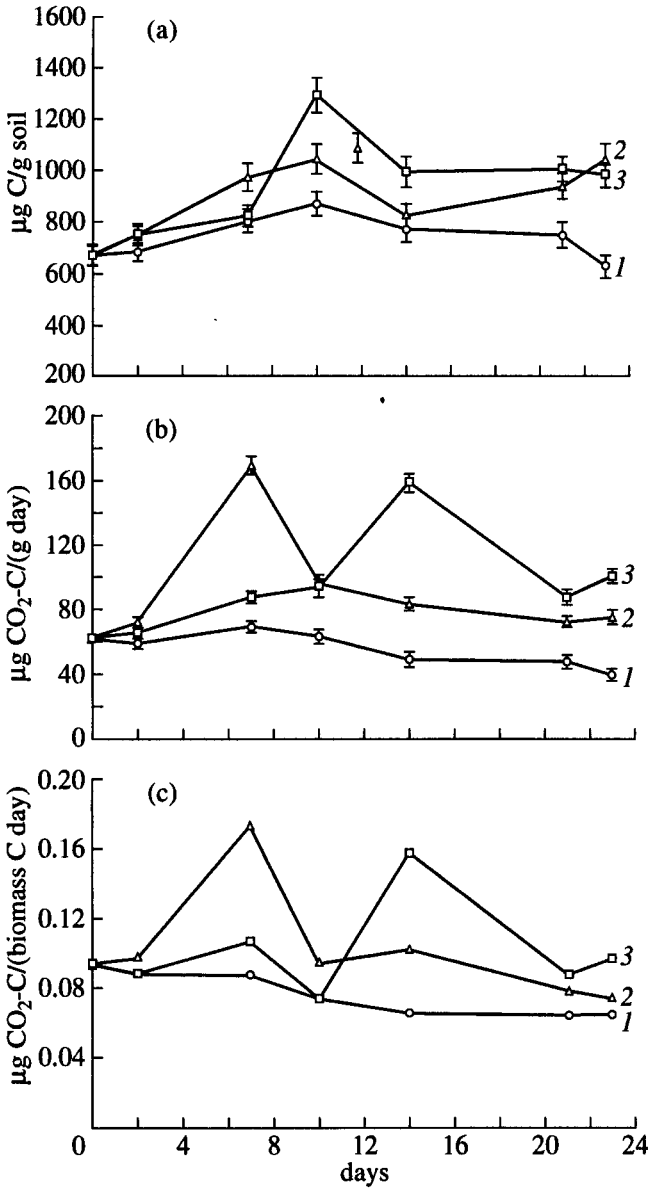

Fig. 2. Microbial biomass dynamics determined (a) by the fumigation-extraction method, (b) from the respiration activity, and (c) from specific respiration measured in the course of decomposition of wheat straw in (*3*) native and (*2*) defaunated soil; (*1*) is control.

out to be similar and ranged from 17.0 to 19.4 and from 17.7 to 21.4 μg CO_2-C/(g day).

The functional diversity of soil microorganisms was not altered by the defaunation procedure employed (Fig. 1).

Effect of microfauna on the dynamics of microbial growth and respiration in the course of wheat straw decomposition. In tests where straw was added to fresh samples of soil, the increase in microbial biomass over the first week was higher in the defaunated test variant, and the peak value of the biomass (1000 μg C/g soil) was observed on the 10th day of incubation. In the presence of nematodes and microarthropods, the initial microbial growth was slower. However, on the 10th day, it reached a maximum of 1300 μg C /g, a value 30% higher than in the soil without animals (Fig. 2a). During the first week, the respiration rate (Fig. 2b) and the specific respiration (Fig. 2c) were higher in the absence of fauna, but later on, both these variables for native soil became larger than the corresponding values for defaunated soil. The difference in the respective absolute values for different variants was, however, fairly small. In soil without straw, the microbial biomass and the respiration rate showed insignificant variation in the course of the test. A similar pattern of biomass and respiration dynamics was observed in the second experiment carried out with soil stored at 12°C for 2 months. In the latter case, the absolute values of the biomass for the soil with animals were 50% higher than in the defaunated soil (data not shown).

In the native soil with straw, the number of nematodes increased by the end of the experiment by a factor of 35 to 52, and the number of microarthropods increased by a factor of 5 to 6. In defaunated soil, nematodes and microarthropods appeared in microcosms only on the 16th to 25th day and their number was much smaller than in the native soil on the same days (Table 1).

It can be concluded, therefore, that the microbial biomass and the respiration activity in soil are trophically controlled by microfauna.

Biomass and respiration rate dynamics in refaunated soil. In order to find out if the observed effects could be due to a nonspecific action of the defaunation procedure (for example, through a change in the physiological state of microorganisms induced by heating), some samples of defaunated soil were refaunated with a natural complex of nematodes and microarthropods extracted from an equivalent quantity of soil. The observed dynamics of microbial biomass and respiration activity tended to be similar to those obtained in the previous experiment. During the first week, both variables were greater in defaunated soil. However, after 10 days, both the biomass of microorganisms and the respiration rate became greater in the soil with microfauna (Fig. 3).

The population of microarthropods failed to recover after defaunation for 15 days of incubation and there was only a minor increase in the number of nematodes (to 36 ± 7 ind./10 g). In the test with reintroduction of nematodes, their number doubled by the end of the experiment (changing from 384 ± 51 to 747 ± 62 organisms/10 g).

Relation between the number of nematodes and their effect on the microbial complex. In order to determine the limits of the trophic activity of the nematode complex governing the production and activities of microorganisms, the number of nematodes was doubled by transferring them to defaunated soil with straw from an equivalent amount of soil. The patterns of the microbial biomass (Fig. 2a) and respiration dynamics (Fig. 2b) observed in the soil with the naturally occur-

Table 1. Microfauna population dynamics in native and defaunated soil

Variant	Fresh soil			Stored soil		
	Days from the test start					
	1	16	25	1	16	25
	Number of nematodes, ind./10 g soil					
Native soil + straw	25 ± 7	34 ± 8	1310 ± 75	43 ± 12	282 ± 27	1517 ± 83
Defaunated soil + straw	0	2	435 ± 62	0	78 ± 17	480 ± 54
Control	25 ± 7	27 ± 5	155 ± 34	43 ± 12	36 ± 8	223 ± 31
	Number of microarthropods, ind./90 g soil					
Native soil + straw						
collembolans	4 ± 3		36 ± 5	2		3 ± 1
mites	5 ± 2		5 ± 1	9 ± 3		61 ± 6
Defaunated soil + straw						
collembolans	0		3 ± 1	0		0
mites	0		5 ± 1	0		8 ± 3
Control						
collembolans	4 ± 3		14 ± 5	2		0
mites	5 ± 2		7 ± 3	11 ± 4		12 ± 5

Table 2. Dynamics of the nematode number in the experiment involving straw decomposition and defaunated soil reinoculation with the natural nematode complex of natural and double population sizes

Variant	Number of nematodes, ind./10 g soil		
	0 days	14 days	19 days
Defaunated soil + straw	0	4	78 ± 40
Natural number of nematodes + straw	214 ± 38	414 ± 51	908 ± 72
(% of stylet nematodes)	10		35–38
Double number of nematodes + straw	450 ± 56	760 ± 40	1340 ± 144
(% of stylet nematodes)	10		40

ring number of nematodes (about 200 ind./10 g) and in the defaunated variant were generally similar to those previously described. However, in the variant with a doubled population of nematodes (about 400 ind./10 g), the maximum microbial biomass amounted only to 59% and the maximum respiration rate to 50% of the corresponding values in the variant with a natural population of nematodes (Fig. 4). With the doubled population of nematodes, the maximum specific respiration rate was nearly half the corresponding value in the variant where their number was natural (0.037 and 0.06 CO_2-C/(biomass C day) on the 14th day, respectively). In tests with the natural number of nematodes, their population increased by the end of the experiment by a factor of 4.2, and in tests with the double number, it increased threefold (Table 2).

It follows that there exists some limit on the number of nematodes such that, above this limit, their influence on the microbial complex changes from stimulating to inhibitory.

Comparison of the effects of nematodes and KNO_3 on the dynamics of biomass and respiration activity of the microbial complex. In order to explore the mechanism by which the microbial complex is controlled by soil fauna, the effects of nematodes and different doses of mineral nitrogen were studied in the course of straw decomposition. A nematode complex and a KNO_3 solution were applied on the 10th day of incubation, when both the microbial biomass and the respiration rate were noted to decrease in defaunated test variants carried out with the addition of straw (Fig. 2). Application of any doses of KNO_3 was observed to cause a considerable increase in the biomass production and in the respiration rate (Fig. 5), indicating that nitrogen at this point was a limiting factor of microbial growth. The response to the introduction of nematodes was most similar with the effect caused by the applica-

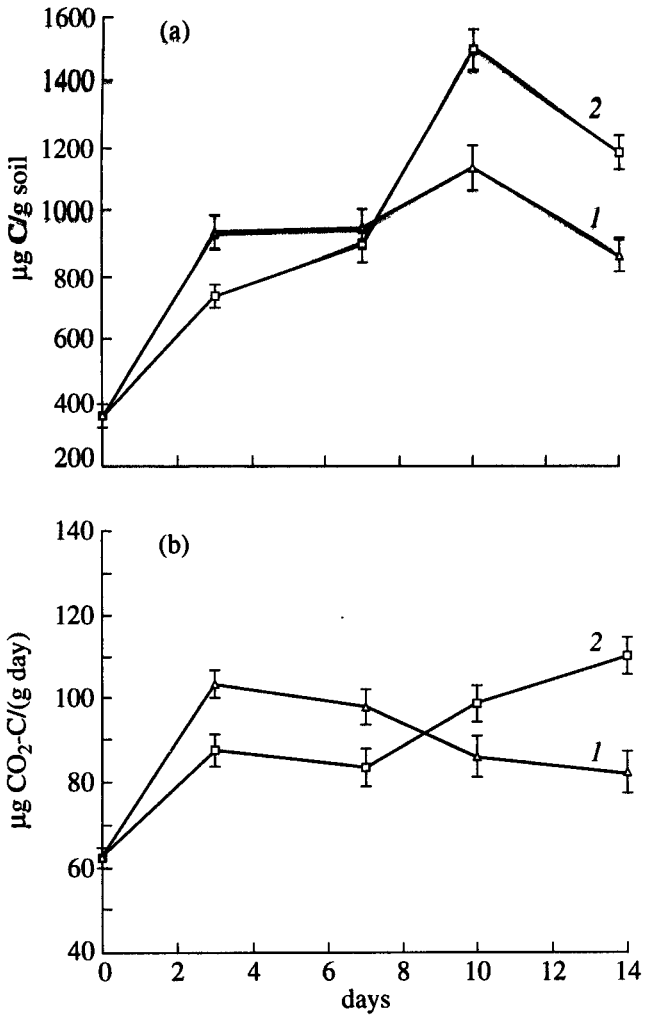

Fig. 3. Dynamics of (a) microbial biomass and (b) respiration activity in refaunated soil in the course of wheat straw decomposition: (*1*) defaunated soil, (*2*) native soil.

tion of 0.78 mg of KNO_3. It is worth mentioning that increased doses of KNO_3 gave rise to proportional increases in the microbial biomass and in the respiration rate. In the variant with nematodes, the maximum specific respiration rate was equal to 0.057 μg CO_2-C/(biomass C day).

Effect of microfauna on the microbial biomass and respiration dynamics in the course of decomposition of alfalfa meal and starch. The effects of microfauna on a microbial complex decomposing nitrogen-rich (alfalfa meal) and nitrogen-free (starch) substrates were studied. The fungal biomass and respiration rate dynamics in the process of starch decomposition were similar to those observed during straw degradation (Fig. 2). In the presence of microfauna, the maximum value of the biomass was 20% higher than in defaunated soil, and the respiration rate was 67% higher. By contrast, in decomposition of alfalfa meal, the peak values of the biomass and respiration rate in native soil were, respectively, 30 and 17% smaller than in the test variants with fauna. This trend persisted through nearly the entire incubation period (Fig. 6).

The dynamics of mineral forms of nitrogen in decomposition of alfalfa meal and starch. By comparing the microbial biomass production with the concentration dynamics of available forms of mineral nitrogen in soil, NH_4^+ (Fig. 7a) and NO_3^- (Fig. 7b), we find that the concentration of mineral nitrogen in soil increases in the course of alfalfa meal degradation; i.e., efficient mineralization of the supplied substrate is under way, and microbial growth is not limited by nitrogen. In the variant with starch added on the 7th day of incubation, the concentrations of both NH_4^+ and NO_3^- decreased to nearly zero values.

After 10 days of starch decomposition in the native soil, the increased fungal biomass and respiration rate matched the increase in the concentration of mineral forms of nitrogen.

DISCUSSION

A conceptual model of trophic regulation of the soil microbial complex by microfauna. The dynamics of microbial growth and respiration activity in soil are controlled by microfauna and can be stimulated or inhibited by 15 to 100% by the trophic activity of animals, depending on their population size and the organic matter composition. The microbial complex is stimulated when nitrogen-free or low-nitrogen organic compounds, such as starch or wheat straw (C : N = 87), are decomposed and when a natural-size nematode population is present. An inhibition of microbial growth and activity is observed when the high-nitrogen alfalfa meal is decomposed (C : N = 28), and the number of nematodes in soil is doubled.

The mechanisms by which microfauna can affect the rates of mineralization, substrate conversion, microbial growth, and microbial respiration are not clear. Based on the results of this work and literature evidence, the regulatory role of microfauna in mineralization of not readily available substrates can be conceptualized as follows (Fig. 8). The predominant part of the microbial complex is inactive, due to the shortage of available nutrient elements [16]. The soil studied contained 12 mg C/g. At the start of the experiment, the soluble organic matter (170–181 μg C/g) constituted only 1.5% of the total organic matter in soil, increasing to 8% (450 μg C/g) after the application of straw. The fraction of microbial biomass carbon in the total organic carbon was initially 3% (350 μg C/g), increasing to 8% (1300 μg C/g) in the course of straw decomposition. It is evident, therefore, that the accumulation of microbial biomass proceeded at the expense of the organic matter applied or at the expense of soil humus.

The effects observed in experiments involving a reintroduction of nematodes alone into defaunated soil

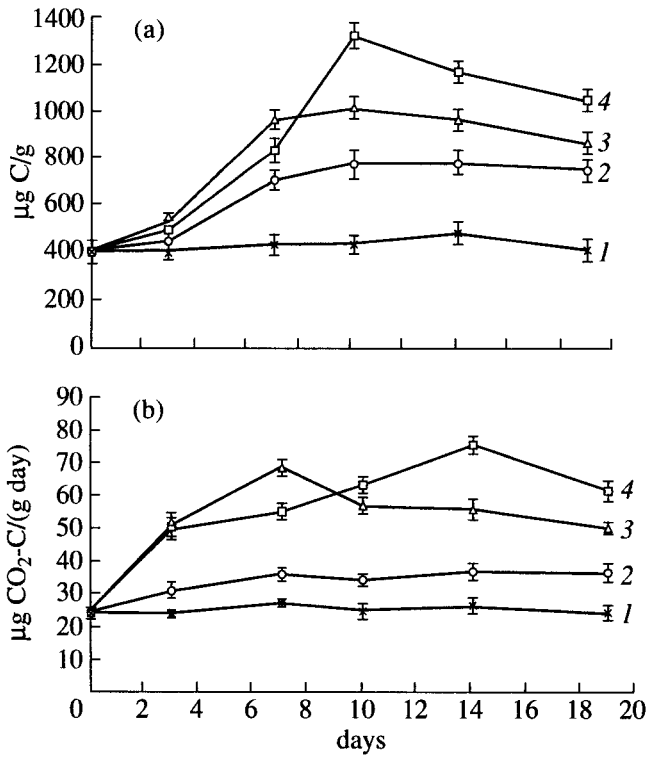

Fig. 4. Dynamics of (a) microbial biomass and (b) respiration activity in soil in the course of wheat straw decomposition with the (*4*) natural and (*2*) doubled numbers of nematodes; (*1*) is control and (*3*) is defaunated soil.

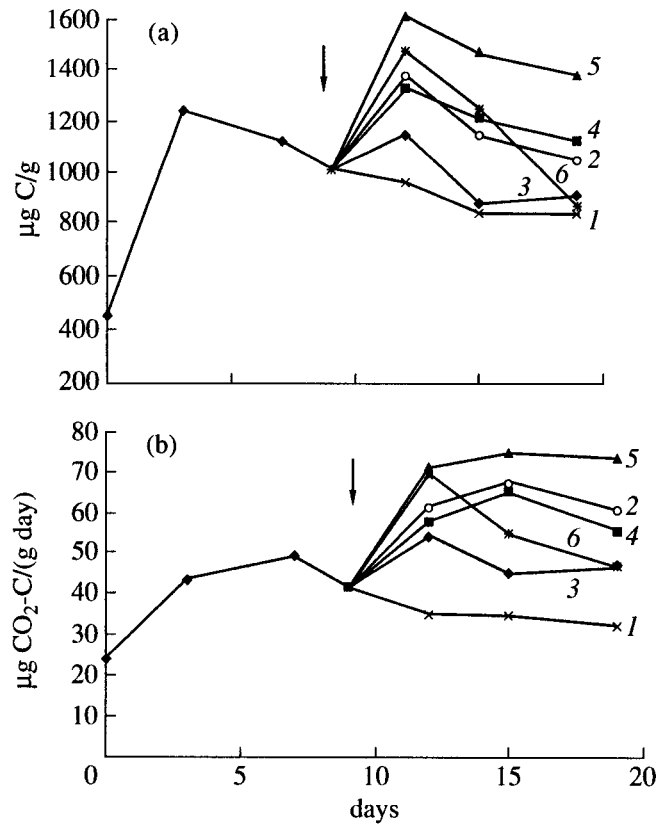

Fig. 5. Effect of nematodes and KNO_3 on (a) microbial biomass and (b) respiration dynamics in the course of wheat straw decomposition. The arrows indicate the points in time when nematodes were introduced or KNO_3 was applied: (*1*) control, (*2*) nematodes, (*3*) 0.35, (*4*) 0.78, (*5*) 2.52, and (*6*) 5.75 mg KNO_3-N/g.

were quantitatively similar to those produced by the entire fauna complex (nematodes and microarthropods). On these grounds, in further experiments, the microfauna in our model was represented only by nematodes.

Nematodes in soil are known to graze on mycelial fungi, yeast, bacteria, and protozoa. The non-stylet forms (bacterivorous and omnivorous) pass microbial cells through their digestive tracts. The stylet forms (fungivorous) perforate mycelium. In the course of microbial biomass utilization, nitrogen forms available to microorganisms are excreted by nematodes into soil along with partially digested or killed microbial cell mass. Piercing mycelium with their stylet at random places, the perforating forms can apparently mortify a large part of a fungal colony by disrupting the system of matter translocation along mycelium. The most vulnerable to such an attack are fungi with coenocytic mycelium. The nematode excretions and the dead biomass in soil constitute an available substrate, and increased concentrations of this substrate are bound to activate more microorganisms and thus result in a greater rate of mineralization of not readily available substrates.

In order to be able to evaluate the contribution of such a positive feedback (in Fig. 8, positive feedback factors are shown by the dashed arrow going from the corresponding block) of microfauna on microbial growth and respiration and, therefore, on the rate of organic matter mineralization, the productions of fauna and microorganisms should be compared. Given in Table 3 are the calculation results for experiments simulating the effect of the natural and doubled populations of nematodes on the microbial complex. According to data available in the literature [17], the dry weight of one bacteria-feeding nematode ranges between 13.6 and 38.1 ng (the mean value is 26 ng dry organic matter or 12 ng C). Adopting this value for our calculations, we find the production of nematodes on the 14th day of incubation to be 0.24 and 0.37 μg/g for a natural and a doubled initial number of introduced nematodes, respectively. The microbial production was, however, 925 and 386 μg C/g, i.e., by three orders of magnitude higher than that of nematodes. It follows that nematodes could utilize only a small fraction of the microbial biomass, liberating only an insignificant part of nutrient elements immobilized in the microorganisms. The results of the experiment do not contradict the ecological pyramid rules. In food webs, the predators (in our case, nematodes) accumulate in their biomass only a small part of the prey crop (microorganisms). In our tests, the biomass of nematodes accounted only

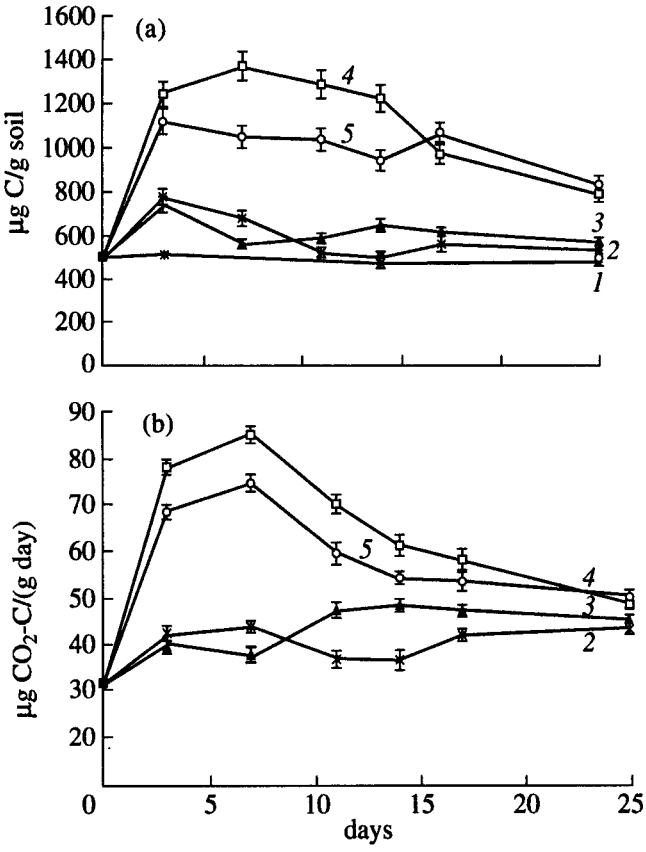

Fig. 6. Dynamics of (a) fungal biomass, determined by the substrate-induced respiration method, and (b) respiration activity in the course of alfalfa meal and starch decomposition: (*1*) control, (*2*) defaunated soil and starch, (*3*) native soil and starch, (*4*) defaunated soil and alfalfa meal, (*5*) native soil and alfalfa meal.

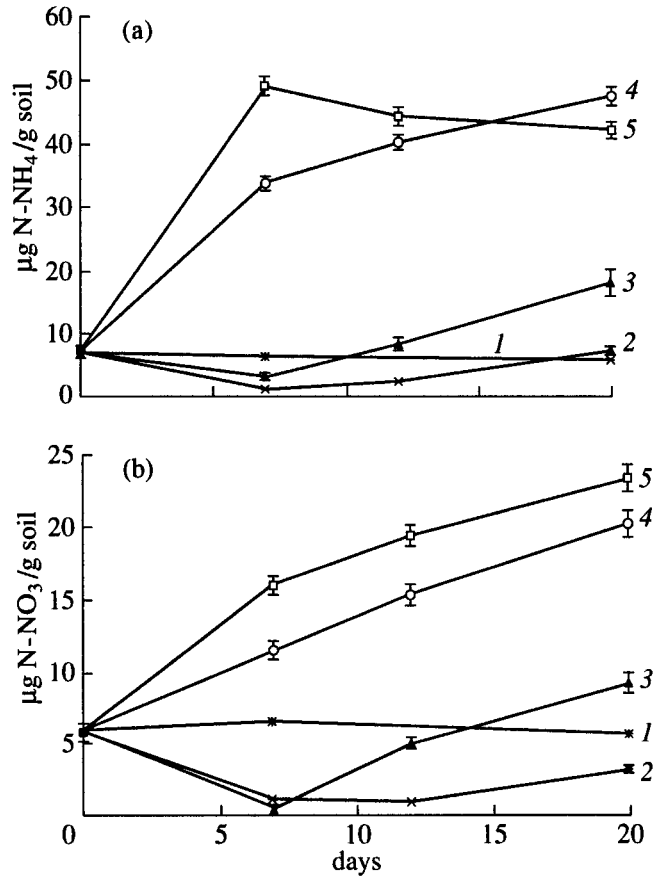

Fig. 7. Dynamics of the concentrations of (a) NH^+_4-N and (b) NO^-_3-N in soil in the course of decomposition of alfalfa meal and starch. For designations, see Fig. 6.

for 0.003–0.01% of the total organic carbon and constituted only 0.1–0.3% of the biomass of microorganisms (0.2–0.6 μg C/g) (Table 3). However, it may well be, that, while grazing, nematodes kill much more biomass than they actually consume. This is especially likely for nematodes grazing on coenocytic fungal mycelium and bacterial cells.

Stimulating effects of nematode introduction were observed to coincide with the results of applying 0.78 mg KNO_3-N. However, this concentration of nitrogen in soil cannot be attained even if all of the microbial biomass were mineralized (on the 10th day, this biomass was equal to 1300 μg C/g). The above arguments make it possible to conclude that the regulation of the production and activity of microorganisms by microfauna cannot be explained by the accelerated cycling of nutrient elements caused by direct grazing.

The obtained evidence seems to suggest that the microbial complex is to a large degree controlled through mechanisms associated with the variation in the activity of microorganisms caused by the trophic activity of microfauna. The positive feedback factors may consist in compensatory growth of microorganisms in response to their grazing by animals, stimulation of microorganisms caused by their passing through the digestive tract, and the action of physiologically active compounds formed by nematodes and entering microbial cells. The compensatory growth of microorganisms was first reported in the interaction of collembolans with fungi [9, 10]. In a binary culture on a nutrient medium, the utilization of part of mycelium from the center of a colony of the fungus *Mortierella isabellina* by the collembolan *Onychiurus armatus* brought about a change from normal growth and sporulation to the formation in the peripheral part of the colony of sectors of fast growing mycelium forming no spores. The activities of hydrolytic enzymes—serine protease and α-amylase—increased by several times in this mycelium. It was assumed that the loss of part of mycelium by the fungus was compensated by a higher rate of growth and higher level of metabolism [10]. Earlier, it was observed that the specific respiration activity of the microbial complex in leaf litter increased in the presence of microarthropods [7]. The hypothesis was that, by grazing dying hyphae, the animals in fact activate fungal growth.

It is an established fact in the community ecology that the trophic activity of animals affects the metabo-

Table 3. Relation between the production of microorganisms and nematodes in the course of decomposition of straw after introduction into defaunated soil of nematodes with the natural and double population size

Test variant	Parameters
No nematodes	
Production of microorganisms over 14 days, μg C/g	617
Natural number of nematodes	
Biomass of nematodes	
1st day of incubation, μg C/g	0.26 (214 ind./10 g)
14th day of incubation, μg C/g	0.50 (414 ind./10 g)
Production of nematodes over 14 days, μg C/g	0.24 (200 ind./10 g)
Production of microorganisms over 14 days, μg C/g	925
Increase in microorganisms production compared to defaunated soil, μg C/g	**+308**
Doubled number of nematodes	
Biomass of nematodes	
1st day of incubation, μg C/g	0.54 (450 ind./10 g)
14th day of incubation, μg C/g	0.91 (760 ind./10 g)
Production of nematodes over 14 days, μg C/g	0.37 (310 ind./10 g)
Production of microorganisms over 14 days, μg C/g	386
Increase in microorganisms production compared to defaunated soil, μg C/g	**–231**

lism of representatives of the preceding levels of the trophic pyramid. For example, it was shown that insect grazing on plant leaves can cause a change in the metabolism of the whole plant and give rise to synthesis of secondary metabolites, resulting in increased production of plant leaves and roots [18]. Utilization of bacteria by protozoa was reported to lead to a 30-fold increase in the bacterial biomass in soil as compared to the test variant without protozoa [19].

The trophic regulation of the microbial complex by fauna depends on the availability of nutrient elements to microorganisms. With a relatively high content in soil of available nutrients, as, for example, in the case of decomposition of alfalfa meal (C : N = 28), microbial growth and mineralization were slowed down by microfauna, whereas, in the case of decomposition of wheat straw (C : N = 87) and starch (no nitrogen), these processes were stimulated (Figs. 2 and 7). It appears that, in the first case, the predominant factor is a direct attack by animals on the active microbial biomass, curbing its growth. In the second case, we apparently have pure compensatory growth. When available nutrient elements are in short supply, organic matter mineralization comes to be stimulated by microfauna.

The population size of microfauna capable of affecting the production of microorganisms can be quite small. In our experiments, the growth and respiration activity of microorganisms was observed to be stimulated by the presence of just 225 nematodes and 10 microarthropods in 90 g of soil (Table 1). It should be mentioned that, in the humus-accumulating horizon, the impact of nematodes on the production of microbial biomass and respiration activity is markedly stronger than that of collembolans and mites. By contrast, the trophic activities of microarthropods are important for the microbial population and the respiration rate in leaf litter [7–9] and in decomposing microfauna excrements [20]. Interestingly, there is a certain optimal number of nematodes such that the microbial production and activity are stimulated by animals. When the number of nematodes exceeds some limit (in our experiments, it was roughly 400 nematodes/10 g soil), the effect of nematodes reverses and the production and activity of the microbial complex come to be restrained (Fig. 4, Table 3). This effect is similar to the so-called *overgrazing*, but, in our view, it cannot be explained by increased grazing intensity, because, as demonstrated by our calculations, the obtained effect is not at all proportional to the amount of microbial biomass consumed by fauna. This can occur only in random microzones with particularly high levels of microorganisms and fauna activity.

The impact of nematodes can, apparently, be out of proportion with the amount of the utilized biomass. Given that, in straw decomposition, the fraction of fungivorous nematodes increased (Table 2), it can be assumed that the number of perforated points on fungal mycelium exceeded some critical level above which the colony is destined to death.

We see, therefore, that neither the stimulating nor inhibiting effect of microfauna changes in proportion with the utilized microbial biomass; these effects appear to be more associated with the induced changes in the physiological state of microorganisms than with

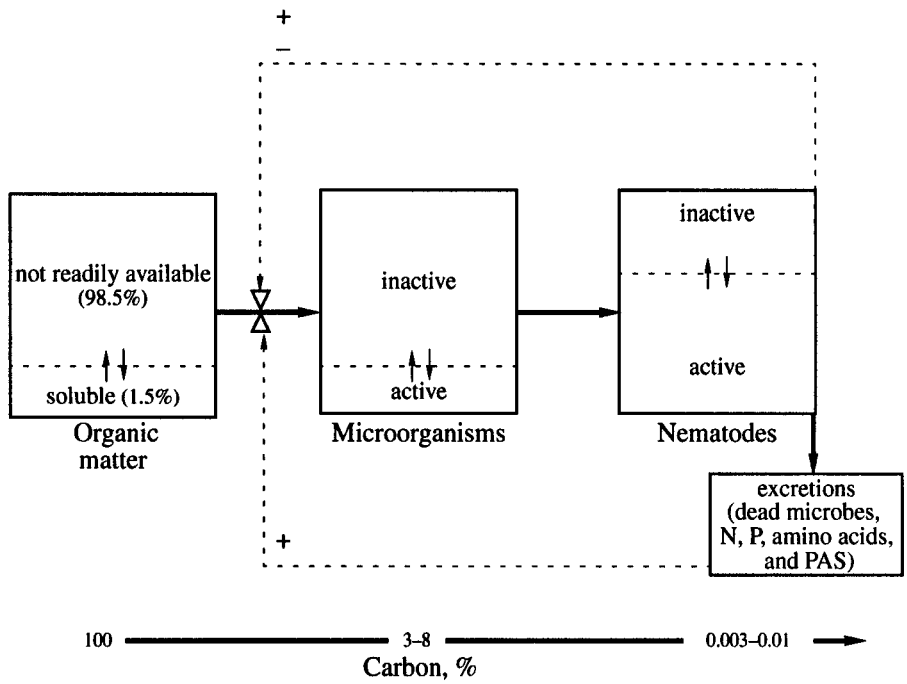

Fig. 8. Conceptual model of the trophic regulation of the microbial complex in soil by microfauna (nematodes). Solid arrows indicate flows of carbon and nutrient elements; broken arrows are (+) positive and (–) negative feedback factors; the "gate" symbol on a solid arrow means that this flow is controlled by the corresponding block indicated by the broken arrow; PAS means physiologically active substances. The positive feedback factors are the direct stimulation of growth and activity of microorganisms caused by consumption of microbial colonies (compensatory growth) and their passing through the digestive tract and by mobilization of nutrient elements (asa result of mycelium perforation or cell death in the digestive tract). The negative feedback factors are growth and activity inhibition caused by overgrazing, which means local extirpation of microorganisms in microzones (mycelium perforation and cell death in the digestive tract).

the mobilization of nutrient elements from consumed microorganisms.

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