EXPERIMENTAL ARTICLES

Microbial Biomass and Growth Kinetics of Microorganisms in Chernozem Soils under Different Land Use Modes

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Abstract—The carbon content of microbial biomass and the kinetic characteristics of microbial respiration response to substrate addition have been estimated for chernozem soils under different land use: arable lands used for 10, 46, and 76 years, mowed meadow, natural forest, and forest shelter belt. Microbial biomass and the content of microbial carbon in humus (C_{mic}/C_{org}) decreased in the following order: soils under forest cenoses— mowed meadow—10-year arable land—46- and 75-year arable land. The amount of microbial carbon in the long-plowed horizon was 40% of its content in the upper horizon of natural forest. Arable soils were characterized by a lower metabolic diversity of microbial community and by the highest portion of microorganisms able to grow directly on glucose introduced into soil. The effects of different scenarios of carbon sequestration in soil on the amounts and activity of microbial biomass are discussed.

Key words: microbial growth kinetics, microbial biomass, carbon sequestration, humus mineralization.

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The maintenance and increase of humus content in soil is a way of sequestration of atmospheric carbon $(C-CO_2)$ in the form of stable organic compounds. It is assumed that this way may reduce the CO₂ content in the atmosphere and diminish the greenhouse effect. There are different opinions and hypotheses as to the possibilities of carbon sequestration due to changed land use, e.g. conversion of arable lands to meadows, or due to an increase of forested areas [1, 2]. The change from conventional tillage to no-till management is an established procedure which contributes to large-scale carbon sequestration in soil [3]. The increase of biocenoses productivity resulting in a greater input of plant residues into soil does not necessarily provide for the formation of stable humus substances, which are preserved in soil for a long time. It has been shown that cultivation of plants in the atmosphere with increased CO_2 content, which leads to a greater input of carbon into soil organic matter, is accompanied by slower formation of stable, long-living organic compounds [4]. Therefore, to choose the optimal strategy of carbon sequestration in soil it is extremely important to know not only the dynamics of total carbon reserves in soil after changing the land use system, but also the retention time of different organic fractions in soil. Alongside with the application of isotopic labeling for assessing the mineralization rate of different pools of organic matter [5], the study of reserves and activity of microbial biomass in soil under changed land use and increased CO₂ content in the atmosphere is no less relevant [6]. It is generally accepted that microbial biomass is the most labile component of soil organic matter, which responds first of all to environmental changes and reflects the trend of accumulation or mineralization of soil organic matter [7]. However, there are rather few studies that not only compare the qualitative composition of soil microorganisms, determining its dependence on agricultural land use or characteristics of the cenoses [8], but also establish the quantitative dependences between the reserves and rates of humus mineralization and the quantity and functional characteristics of microbial biomass. Previously it has been shown [9] that different systems of fertilizers affect the kinetic characteristics of growth and the dominating ecological strategy of microbial communities of arable soils. Obviously, quantitative assessment of the functional characteristics of microbial biomass will contribute to a better understanding of the characteristics of the carbon cycle in arable soils used for different periods of time and in fallow soils that have been out of intensive land use for different periods of time.

The goal of this work was to compare the reserves and activity of microbial biomass and the growth characteristics of microbial communities for chernozem

Experimental variant	Humus, %	pH aqueous	Ca ²⁺	Mg ²⁺	P_2O_5	K ₂ O
			mg-equiv/100 g of soil		mg/100 g of soil	
Forest shelter belt, 105 years	7.0	6.1	42.1	8.7	10.2	50.6
Natural forest, 92 years	8.1	7.0	42.1	8.8	11.1	51.3
Mowed meadow, 118 years	8.7	7.1	41.9	7.9	10.8	50.8
Arable land, 10 years	7.2	7.4	27.8	4	8.5	48.2
Arable land, 46 years	6.2	7.1	28.2	4.3	8.3	47.8
Arable land, 76 years	6.9	7.4	37.4	7.3	8.4	46.3

Table 1. Chemical characteristics of the 0-20-cm horizon of Haplic chernozem (Kamennaya Step) under different land use

soils under conditions of different land use. It was necessary to determine how the duration of tillage or the time after conversion from arable to fallow land would affect the ratio between active and total microbial biomass and the ratio between the pools of total organic carbon and microbial biomass carbon.

MATERIALS AND METHODS

The properties of the microbial pool were comparatively assessed in the chernozem soils of the long-term stationary experiment of the Dokuchaev Research Institute of Agriculture of the Central-Chernozem Belt (Kamennaya Step, Voronezh oblast). Soils of the same type (Haplic chernozem) in different variants of the experiment differed in their properties due to the duration of anthropogenic impact (plowing, mowing) [10]. The quantity of microbial biomass and the kinetics of respiration response to substrate addition were determined for arable soils used for 10, 46, and 76 years, as well as for the plot of mowed meadow (with the regime maintained for 118 years). As control plots, we selected a forest shelter belt (planted forest, 105 years old) and natural forest (92 years old). The chemical characteristics of the soils are given in Table 1.

Soil samples taken in early May from the 0–20-cm layer were sieved (diameter, 3 mm), cleared from roots and large plant residues, moistened to 50% water holding capacity (WHC), and kept in refrigerator at 4–6°C before the beginning of experiments (for 2–3 months). Prior to measurements, the soil was incubated at room temperature for 1–2 days.

The kinetics of microbial growth induced by substrate addition into soil was determined by measuring the rate of CO_2 emission. For this purpose, 10-g soil portions were moistened to 60% of WHC and homogenized in a mixer together with the mixtures of talcum and glucose (4 mg C/g soil) or talcum and yeast extract (40 mg C/g soil) supplemented with mineral salts (mg/g): $(NH_4)_2SO_4$, 1.9; K₂HPO₄, 2.25; and MgSO₄ · 7H₂O, 3.8; the rate of CO₂ emission was measured in a flow gas analyzer [11].

The maximal specific rate of microbial growth (μ_m, h^{-1}) was determined by approximation of the experimentally obtained values of the rate $(v, \mu g C (g \text{ soil})^{-1} h^{-1})$ of CO₂ emission according to the equation [12]:

$$v = v_0^{\rm pr} \times \exp(\mu_{\rm m} t) + v_0^{\rm fut}, \qquad (1)$$

where $v_0^{\rm pr}$ was the initial rate of productive substrate

oxidation coupled with ATP synthesis; v_0^{fut} was the initial rate of futil respiration; and *t* was the time. The parameters of Equation (1) providing the best fit of the experimental data and the calculated curve were selected using ModelMaker 3.1 software package (Cherwell Scientific Publishing Ltd) by the least-squares method.

Approximation was made only with the part of the microbial growth curve that provided maximal values for statistic criteria Q and r.

The content of *biomass of soil microorganisms capable of immediate growth* on added glucose was calculated using the parameters found for Equation (1). The coefficient of the physiological state of microorganisms (r_0) was calculated from the ratio of futile and productive respiration rates:

$$r_0 = v_0^{\rm pr} \times 0.1 / (v_0^{\rm fut} + v_0^{\rm pr} \times 0.1).$$
 (2)

In this case, the content (in percentage terms) of microorganisms capable of immediate growth will be $r_0 \times$ 100. A detailed explanation and substantiation of the above calculations has been published previously [12, 13].



Fig. 1. The content of microbial biomass carbon (1) and DNA (2) in chernozem soils under different farm lands.

Duration of the lag period (t_{lag} , **h**) in the respiratory response characterizes the time interval when the respiration rate enhanced after glucose addition remains at a constant level, i.e. when there is no active growth of microorganisms. The moment of time when the increasing rate of growth (productive) respiration v_0^{pr} becomes equal to the rate of futile respiration v_0^{fut} [14] was considered as the beginning of growth (end of the lag period); i.e.,

$$t_{\rm lag} = \ln(v_0^{\rm fut}/v_0^{\rm pr})/\mu_{\rm m}.$$
 (3)

Calculation of auxotroph index. On the basis of the measured specific rates of microbial growth in soil after the addition of glucose–mineral mixture or yeast extract, we have calculated the *index of auxo-trophic-ity* as a quotient obtained from division of the maximal specific microbial growth rates on glucose and yeast extract (μ_{vl}/μ_{ve}) [14].

Calculation of the total microbial biomass. Based on the values of intensity of the initial respiratory response $(v_0^{\text{pr}} + v_0^{\text{fut}})$ obtained by selection of the parameters of Equation (1), *the total microbial biomass* was calculated by *the method of substrate-*

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induced respiration (SIR), C_{micr} (µg (g soil)⁻¹), using the ratio

$$C_{\rm micr} = 1.89 \times 40.04 \times (v_0^{\rm pr} + v_0^{\rm nut}), \tag{4}$$

according to the previously established dependence [15].

DNA quantity in soil was determined by an optimized procedure of direct quantitative extraction as described previously [16]. It included mechanical, enzymatic, and thermal impact on microbial cells. The quantity of double-stranded DNA was determined by the fluorescence intensity of a PicoGreen solution (PicoGreenTM, Molecular Probes), a highly specific and very sensitive reagent.

Determinations were made in four (DNA), three (microbial biomass and basal respiration of soil), and two (kinetic growth parameters) repetitions.

RESULTS AND DISCUSSION

The Content of Total Microbial Biomass and the "C microbial : C organic" Ratio

Figure 1 shows the change of the content of microbial carbon determined by SIR and the content of DNA in the upper (0–20 cm) horizon of chernozem depending of the duration and type of land use. The maximal quantity of microbial biomass was revealed in soils



Fig. 2. The content of microbial biomass carbon as a component of humus carbon (C_{mic}/C_{org}) in some chernozem soils under different farm lands.

under forest vegetation: forest shelter belt and natural forest. These biocenoses are characterized by large amounts of incoming tree litter, large reserves of available organic matter, and the developed microbial community structure [8]. In the soils of mowed meadow land, the quantity of microbial biomass decreased but still significantly exceeded that in the arable soil. The soil tillage resulted in the decrease of the content of the total microbial biomass. The decrease of microbial carbon by a quarter as compared with its reserves in the meadow land soil was already observed 10 years after ploughing up. In the next 36 years, the content of the total microbial biomass decreased further (to 40% of its amount in the soil of non-mowed fallow land), which was consistent with the decrease of humus content in the studied variants (Fig. 1, Table 1). The duration of using chernozem for tillage had a significant effect: the content of microbial biomass in the 46- and 76-year arable land was almost 2 times lower than in the 10year arable land. After 76 years of plowing, there was no decrease of total biomass as compared with the variant of arable land after 46 years of use. Both the decrease of the total microbial biomass and the rate of humus mineralization became slower after 50 years of chernozem tillage. The data on microbial biomass obtained by the SIR method are in good agreement with the DNA quantity in soil (Fig. 1). The coefficient of linear regression between these indices was 0.995 with a high level of probability (F < 0.0001). The coincidence of two alternative methods, the results of which are a measure of the quantity of the total microbial biomass in soil, enhances the reliability of our conclusions. At the same time, the absolute values of microbial carbon content in soil calculated on the basis of SIR depend to



Fig. 3. Interrelation between the microbial biomass quantity and total carbon content in soil for some chernozem soils under different land use. Circles designate arable lands, triangles designate fallow lands, and hollow symbols are for soils under forest vegetation.

a great extent on the value and reliability of the scaling factor (in our case, 40 according to [15]), which is, strictly speaking, not a constant for different soils [13].

The portion of microbial biomass as the humus component (C_{mic}/C_{org}) decreased in the following order: forest shelter belt-natural forest-mowed meadow land—10-year arable land—46-year arable land—76year arable land (Fig. 2). This ecophysiological coefficient is usually associated with the stability of a microbial community and soil as a whole [17, 18]. The example of the studied chernozem soils distinctly shows that the increase of anthropogenic impact results in the decrease of resistance of microorganisms to the action of disturbing factors. Comparison of the obtained order with the content of humus in chernozems (Table 1) suggests the conclusion that the decreased fraction of the total microbial biomass in the humus indicates decreasing humus content and predominance of mineralization processes. However, this conclusion is true only in the range of soils with the common type of plant cover (mowed steppe and arable land). The changed character of the biological cycle in a forest biocenosis (overgrowing of meadow land) resulted in the increase of the $C_{\rm mic}/C_{\rm org}$ ratio as compared with the mowed meadow land (Fig. 2) and mineralization of some part of humus (Table 1, Fig. 3). Two opposite tendencies can be observed (shown by arrows in Fig. 3): (1) the coupled increase of microbial biomass and humus quantities under conversion of arable land into steppe biocenosis (mowed meadow land) and (2) decrease of humus reserves in soil, which occurs simultaneously with the increase of total reserves of microbial biomass under fallow land overgrowing and forest aging. Ecological and climatic conditions are determinative in this case.

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rest can- C-CO₂, μ g g⁻¹h⁻¹

Higher amounts of moisture in soil under the forest canopy contribute to more complete mineralization of organic matter and retardation of humification. At the same time, the lack of moisture in steppe results in predominance of the humification process. Our results for forest soils correlate with the tendency of increase in the C_{mic}/C_{org} ratio with forest aging, which has been revealed in the work of Anderson [19]. In conclusion, it should be noted that the ecophysiological coefficient C_{mic}/C_{org} may be an additional useful index of the intensity of the biological cycle in soil-plant systems for some of the soils under study. The C_{mic}/C_{org} ratio increased with the decrease of anthropogenic impact on chernozem soils. The quantity of microbial biomass per unit of humus characterizes the intensity of the carbon turnover in soil. In soils with great annual input (and mineralization) of plant material, more microbial biomass is formed per unit of organic matter.

Kinetics of the Respiratory Response and Active Microbial Biomass

Figure 4 presents the data on the change of the respiration rate in soils enriched with a mixture of glucose and mineral salts. In general, respiration rate in the samples of chernozem soils under forest shelter belt and fallow land increased more quickly than in the samples of plowed chernozem soils. The curves for natural forest and 10-year plowed chernozem were distinguished in each of these two groups (Fig. 4a and 4b), respectively. The time of attaining the maximal respiration rate and peak height (easily distinguishable visually) depended on initial respiration rate and microbial growth rate. Therefore, the observed differences can be best assessed after quantitative mathematical description of the kinetics of soil respiration. For each of the studied variants, Table 2 gives the values of the param-



Fig. 4. The dynamics of respiratory response of microorganisms after introduction of glucose-mineral mixture into chernozem. in (a) fallow lands and (b) arable lands. Experimental and calculated values of respiration rate (Equation 1, Table 2) are represented by symbols and curves, respectively: mowed meadow (1); natural forest (2); forest shelter belt (3); 76-year arable land (4); 46-year arable land (5); 10-year arable land (6).

eters $(\mu_m, v_0^{fut}, v_0^{pr})$ at which Equation (1) describes the experimental data in the best way, as well as the amount of microbial biomass responding to glucose

Experimental plot	Maximal specific rate	Initial respiration rate, $\mu g C g^{-1} h^{-1}$		Microbial biomass, kinetic method, $\mu g C g^{-1}$		Lag period h
	of microbial growth, μ_{max} , h^{-1}	futile, v_0^{fut}	productive, $v_0^{\rm pr}$	growing	sustaining + growing	Lag period, if
Forest shelter belt	0.46 (0.02)	11.11 (0.43)	0.22 (0.047)	0.48 (0.120)	237 (1.11)	8.41 (0.17)
Natural forest	0.56 (0.01)	10.98 (0.06)	0.15 (0.028)	0.27 (0.056)	193 (3.51)	7.58 (0.16)
Mowed meadow	0.49 (0.007)	9.69 (0.04)	0.14 (0.009	0.29 (0.022)	194 (1.93)	8.5 (0.02)
Arable land, 10 years	0.56 (0.03)	7.11 (0.55)	0.13 (0.024)	0.23 (0.057)	124 (2.06)	7.0 (0.04)
Arable land, 46 years	0.40 (0.025)	3.25 (0.22)	0.19 (0.076	0.46 (0.155)	79.68 (10.06)	7.0 (1.57)
Arable land, 76 years	0.48 (0.012)	3.82 (0.08)	0.16 (0.007	0.35 (0.005)	81.10 (0.51)	6.64 (0.22)

Table 2. Kinetic parameters of microbial growth in the upper horizon (0–20 cm) of Haplic chernozem after soil enrichment with glucose (standard deviation values are given in parentheses)

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Fig. 5. The percentage of growing microorganisms in the total biomass reacting to glucose introduction into chernozem soils at different farm land use (a) and interrelation between the contents of growing microorganisms and total organic carbon in chernozem (b).

addition. Specific rates of microbial growth (μ_m) were the highest for soil with the shortest period of tillage (among arable soils) and for natural forest (among nonarable chernozem soils). These results are in agreement with the theory of Odum [20], according to which the growth rate of organisms must decrease in more mature biocenoses.

The lesser percentage of growing microbial biomass in non-arable chernozem soils (Fig. 5a, Table 2) suggests a steady equilibrium between the input and mineralization of organic matter in these soils. Permanent tillage in the long term results apparently in additional enrichment of soil with available organic carbon due to humus mineralization. This, in turn, changes the structure of soil microbial community, increasing the portion of growing biomass. The negative relationship



Fig. 6. The value of the auxotrophicity index in chernozem soils under different land use.

between the quantity of active microbial biomass and the content of organic carbon in the upper chernozem horizon is shown in Figure 5b. Duration of the lag period (t_{lag}) was higher for non-arable chernozem soils. This characteristic was less for all plowed plots. Such changes could be explained by the greater quota of productive respiration as compared with the futile one in plowed plots (see also Fig. 5a), which suggests different structures of microbial communities in these soils.

The conclusion about the differences in the functional activity of microbial communities of chernozem soils under different agricultural use is confirmed by comparison of the indices of auxotrophicity for the studied soils (Fig. 6). Their values may be a gauge of metabolic diversity of a microbial community. The increase of the auxotrophicity index in the samples of chernozem soils used as arable land for 46 and 76 years is evidence of decreasing metabolic diversity of microbial community at long-term tillage.

Thus, at conversion of arable lands into fallow lands, both the content of humus carbon and the quantity of microbial biomass in soil increase. The difference for the arable variant (46 years of use) and the chernozem soils of fallow plots is presented in Figure 7. It is obvious that the accumulation of carbon as a component of microbial biomass and humus proceeds disproportionately on different fallow lands; this is also easily seen in Figure 2. The soil under mowed meadow accumulates more humus as compared with chernozem soils under forest vegetation, which is associated with the lesser part of microbial biomass as a component of mowed meadow humus. The biomass of the heterotrophic portion of the microbial community determined by the SIR method is probably responsible for the processes of mineralization of soil organic matter. This conclusion is illustrated well by the inverse rela-



Fig. 7. The relative increase of carbon content in humus and microbial biomass under conversion of chernozem soils from arable lands into meadow lands. Light sites: increase of biomass; shaded sites: increase of humus.

tion between the fraction of active biomass and the quantity of organic C in chernozem soils (Fig. 5b). In this respect, carbon sequestration at conversion of arable lands into meadows or steppe seems to be more reliable, because carbon accumulates in long-living humus compounds; this is particularly true for the humus of chernozem. On the other hand, the higher amount of carbon in forest biocenosis can accumulate as a component of plant biomass. Therefore, the choice of strategy of carbon sequestration must depend both on the planned rate and reserves of carbon burial and on the predicted changes of temperature-moisture conditions of biocenosis formation. Under climate humidification and the overgrowing of fallow land with forest, the amount of carbon in soil may increase not as significantly as in fallow land chernozem soils under steppe.

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