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SOIL CHEMISTRY

The Reserves of Carbon in Vegetative and Microbial Biomass of Siberian Ecosystems

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Abstract—Extensive factual data on the reserves of labile organic carbon in the vegetative matter and microbial biomass of nonforest ecosystems of Siberia have been analyzed. It is shown that the highest reserves of labile carbon are typical of virgin and mown meadow ecosystems in the flood plains of Western Siberia. The lowest reserves of labile carbon are found in cereal agrocenoses of central and Eastern Siberia. The reserves of microbial biomass vary by an order of magnitude (from 50 to 500 g/m^2) and depend on the type of land use. They increase with an increase in the degree of soil moistening and heat supply. Maximum changes in the reserves of labile carbon take place upon the transformation of natural forest and steppe cenoses into agrocenoses. Within 200 years of soil cultivation in Western Siberia, the net primary production of lands occupied by agrocenoses has decreased by three times; the reserves of vegetative matter, by six times; and the reserves of soil organic matter (0–20 cm), by 30%.

INTRODUCTION

Vegetative matter (VM) and microbial biomass (MB) are important components of the easily mineralizable organic matter in virgin and agricultural ecosystems [15]. In virgin meadow-steppe ecosystems of Western Siberia, these fractions constitute about 13% of the total pool of vegetative and soil organic matter and 22% of the pool of easily mineralizable (labile) organic matter. In agrocenoses developing in the place of former meadow steppes, the sum of VM and MB decreases to 8% of the total pool of organic matter, though their share in the reserves of labile organic matter remains at the same level as in virgin ecosystems (22%) [17]. All the fractions of organic matter in virgin ecosystems are derived from vegetative matter in the course of its transformation. The transformation of vegetative matter by soil microorganisms—bacteria and fungi—is the main factor of humus accumulation and mineralization of organic substances. In this context, information about the reserves of the phytomass, dead mass (plant remains), and microbial biomass gives us quantitative estimates of the sources of partly and completely transformed fractions of the organic matter.

Under the impact of human activity, considerable changes in the reserves of VM and MB take place over vast areas, which affects the global carbon cycle. In order to have quantitative estimates of these changes, it is necessary to have data on the average reserves of VM and MB in virgin and human-modified ecosystems, as well as on the areas occupied by these ecosystems.

The aim of this study is to determine the reserves of organic carbon bound in vegetative matter (C_{VM}) and microbial biomass (C_{MB}) in Siberia, to analyze correlative relationships between these parameters, and to assess the changes in the carbon cycle resulting from alteration in the land use pattern within the last 150 years.

METHODS

The methods of organic carbon determination in VM and MB were described in out previous work [17]. The carbon of microbial biomass was determined by the method of fumigation and incubation [24]. The length and mass of fungal mycelium and the mass of micromycetal spores were determined by the method of membrane filters modified by Demkina and Mirchink [3]. The amount of carbon in postharvest plant remains was calculated from data on crop (grain) yields by means of specially developed regression curves displaying the dependence of postharvest remains and the carbon content in them on grain yields. For Central Siberia, these curves were obtained from the data published by Chuprova [21]. We failed to find similar data for the territory of Eastern Siberia. In the latter case, we used regression equations developed for western and Central Siberia.

RESULTS AND DISCUSSION

The territory of southern Siberia (from the southern boundary of Russia to 60° N) can be divided into three sectors: western, central, and Eastern Siberia. Western Siberia includes the Altai region and Novosibirsk, Kemerovo, Omsk, Tomsk, and Tyumen (without northern national districts) oblasts. Central Siberia comprises the

Table 1. Number of Siberian ecosystems for which the determinations of the pools of labile organic carbon are available

Ecosystems	Vegetative matter	Total microbial biomass	Fungal biomass
Agrocenoses	231 (3330)	31	16
including grain croplands	160 (1500)	21	5
Hayfields	50 (100)	20	13
Pastures	82 (131)	21	12
Virgin and idle meadows and steppes	69	18	12
Forests and bogs	No data	14	23
Total	132 (3561)	104	76

In parentheses, the number of ecosystems characterized by incomplete data is given.

Krasnoyarsk administrative region (without national districts) and the republics of Khakassia and Tuva. Eastern Siberia includes the Irkutsk and Chita oblasts and the Buryat Autonomous Republic.

The values of C_{VM} and C_{MB} were separately assessed for herbaceous ecosystems and agrocenoses. The first group included virgin and long-fallow ecosystems, hayfields, and pastures; the second group comprised grain and forage agrocenoses and fallow fields.

Statistical data on the reserves of C_{VM} and C_{MB} are very uneven (Table 1). The most complete information is available for the territory of Western Siberia. Data on the contents of C_{VM} and C_{MB} in the ecosystems of Central Siberia are rather scarce; still less information is available on the ecosystems of Eastern Siberia. Most of the materials concern data on the yields of main crops; data on subsidiary crops and on the amounts of postharvest residues and roots are less complete. Minimum information is available on the reserves of dead vegetative mass (mortmass) in the soils of different agrocenoses. For Eastern Siberia, these data are virtually absent. Though data on virgin herbaceous ecosystems are not very numerous, they offer all the information required to assess the reserves of C_{VM} and C_{MB} [4–6, 13, 14, 20]. The amount of data on the microbial biomass is 40 times lower than that on the vegetative matter, which attests to the insufficient study of the role of microbial biomass in soils and ecosystems.

The Reserves of Vegetative Matter

Herbaceous ecosystems occupy 22000000 ha, or 25% of the total area in the studied regions of Western Siberia; 12000000 ha (18%) in Central Siberia; and 9000000 ha (6.5%) in Eastern Siberia. These ecosystems occupy minor areas in the zones of taiga and deciduous forests where they are almost completely used for pasturing and hay making. In the forest-steppe zone, herbaceous (steppe and meadow) ecosystems occupy nearly 35% of the territory. Most of them (60%) are used as pastures and hayfields. About 40% of herbaceous ecosystems in the forest-steppe zone are represented by long-fallow lands, solonetzic steppes, and solonchakous meadows. The area of herbaceous ecosystems in the steppe zone comprises more than 50% of the territory. Nearly 40% of steppe ecosystems, especially in the subzone of dry steppes, are subjected to such minor anthropogenic loads that they may be considered virgin steppes. Flood-plain meadows are mainly used as hayfields; however, the main area of flood-plain meadows lies in the northern scarcely populated part of the territory so that these meadows may remain unmown for many years. The total area of hayfields and pastures in Siberia is assessed at 28718000 ha (1991); about 11% of them occur in the areas that were previously covered by forests.

The obtained materials allow us to characterize virgin meadows, hayfields, and pastures in all natural zones of southern Siberia with respect to the reserves of vegetative matter in them. The total pool of vegetative matter can be subdivided into several fractions: green phytomass, twigs, litter, and live and dead underground parts of plants (within the layer of 0–20 cm). The reserves of green phytomass are calculated for the stage of its maximum development before mowing. This information for Western Siberia is available from our previous paper [17]. Data on central and Eastern Siberia are summarized in Table 2. According to averaged data (Table 3), the content of C_{VM} in herbaceous ecosystems of Siberia varies from 600 to 1400 g/m^2. Maximum values are observed in virgin flood-plain meadows of Western Siberia; minimum values are typical of flood-plain meadows in Eastern Siberia. Mowing loads on flood-plain meadows somewhat decrease the reserves of C_{VM} in Western Siberia; in Eastern Siberia, the effect of mowing is quite the reverse: the reserves of C_{VM} on regularly mown hayfields are almost two times higher than those on unmown hayfields. The same tendency is observed for the other types of herbaceous ecosystems: anthropogenic loads on them lead to a decrease in the reserves of C_{VM} in Western Siberia; in more cold and continental ecosystems of Eastern Siberia, anthropogenic loads often lead to an increase in the content of C_{VM}. The latter fact is explained by a considerable increment in the reserves of dead underground biomass (mortmass) in conditions of the impeded mineralization of plant remains upon soil compaction (owing to mechanical pressure) and cold soil temperatures.

Agrocenoses occupy the areas of 19500000, 4769000, and 4467000 ha in the territories of western, central, and Eastern Siberia, respectively. The share of agrocenoses in the total land reserves in Western Siberia constitutes about 19%, decreasing to 3% in Eastern Siberia. Grain crops are cultivated on about 58% of plowed territory; forage crops (forbs and corn for silo), on 28%; and potatoes, vegetables, and some industrial

Table 2. The C_{VM} content (g/m^2) in herbaceous ecosystems of Central and Eastern Siberia

Region, ecosystem, type of land use	*n*	G	T + L	R (0–20 cm)	UVR (0–20 cm)	VM
Central Siberia						
Herbaceous mires and swampy meadows, the Nazarovo Depression						
Virgin plots	4	365 (50)	276 (52)	350 (46)	1622 (250)	2613
Flood-plain meadows on meadow alluvial soils, the Nazarovo Depression						
Virgin plots	5	111 (6)	120 (40)	399 (38)	508 (51)	1138
Hayfields	5	134 (21)	92 (12)	433 (38)	536 (14)	1195
Pastures	1	50	72	388	504	1014
Mesophytic meadows on gray forest soils, the Nazarovo Depression						
Virgin plots	8	141 (13)	101 (22)	338 (44)	495 (69)	1076
Hayfields	1	168	76	266	410	920
Mesophytic meadows on meadow and meadow-chernozemic soils Nazarovo Depression						
Virgin plots	4	115 (21)	75 (15)	266 (46)	365 (55)	821
Hayfields	1	281	156	312	759	1544
Pastures	5	87 (10)	56 (8)	296 (31)	260 (81)	698
Tuva intermontane basins						
Hayfields	1	108	39	528	193	867
Salt-affected meadow ecosystems Southern Minusinsk Depression						
Pastures	1	105	72	692	613	1482
Tuva intermontane basins						
Pastures	2	80	49	504	388	1020
Meadow steppes on leached and ordinary chernozems Nazarovo Depression						
Virgin plots	5	127 (22)	133 (22)	298 (43)	421 (80)	979
Hayfields	4	174 (15)	119 (7)	443 (139)	357 (67)	1092
Tuva intermontane basins						
Pastures	3	60 (90)	83 (11)	580 (371)	1003 (110)	1724
True steppes on ordinary and southern chernozems and on dark chestnut soils Nazarovo Depression						
Pastures	3	126 (11)	100 (24)	516 (94)	741 (72)	1482
Southern Minusinsk Depression						
Virgin plots	3	84 (12)	125 (52)	504 (34)	509 (135)	1221
Pastures	6	50 (12)	46 (8)	401 (62)	558 (94)	1055
Tuva intermontane basins						
Virgin plots	2	80	341	531	758	1709
Pastures	7	52 (6)	41 (7)	456 (72)	468 (97)	1017
Dry steppes on chestnut soils Tuva intermontane basins						
Virgin plots	5	37 (3)	95 (8)	307 (37)	337 (61)	776
Pastures	16	42 (4)	59 (7)	372 (21)	347 (41)	820

Table 2. (Contd.)

Region, ecosystem, type of land use	*n*	G	T + L	R (0–20 cm)	UVR (0–20 cm)	VM
Eastern Siberia, Cisbaikal region						
Flood-plain meadows on meadow alluvial soils						
Tuva intermontane basins						
Virgin plots	3	157 (47)	68 (13)	191 (32)	571 (85)	987
Pastures	4	46 (15)	35 (12)	126 (24)	155 (28)	362
Petrophytic steppes;						
Minusinsk Depression						
Pastures	3 1	101 (20)	112 (42)	557 (31)	664 (144)	1433
Eastern Siberia, Cisbaikal region						
Flood-plain meadows on meadow alluvial soils						
Virgin plots	1	122	40	201	196	559
Hayfields	1	164	56	266	266	752
Pastures	1	126	28	418	420	992
True steppes on ordinary chernozems						
Pastures	1	30	24	105	159	318
Psammophytic steppes						
Pastures	1	25	34	155	214	427
Eastern Siberia, Transbaikal region						
Meadow steppes on leached and ordinary chernozems						
Pastures	2	51	48	409	800	1323
True steppes on powdery-calcareous chernozems and dark chestnut soils						
Virgin plots	2	51	48	255	266	620
Pastures	10	37 (5)	31 (6)	324 (32)	783 (50)	1174
Dry steppes on chestnut soils						
Pastures	5	31 (3)	54 (5)	337 (25)	543 (53)	965

Error of the mean is given in parentheses. Designations: (*n*) number of ecosystems, (G) green phytomass, (T + L) twigs and litter, (R) live roots, (UVR) underground vegetation remains, and (VM) vegetation matter (total).

crops, on 3%; about 11% of plowlands are under fallow. Spring wheat is the main grain crop. Most of the available data on crop yields have been obtained at strain-testing stations and experimental farms [1, 10, 22]. As a rule, the yields obtained at strain-testing stations and experimental farms are two times higher than the yields obtained by ordinary farms, including collective farms (kolkhozes and sovkhozes). For instance, in conditions of the experimental crop rotation studied by the Krasnoyarsk Research Institute of Agriculture, average (for 10 years) yields of wheat grain reached 2.5–3.0 t/ha immediately after the fallow stage, 1.7–2.0 t/ha on the second year after fallow, and 1.2–1.4 t/ha on the third year after fallow [22]. Average grain yields obtained at strain-testing stations from 1976 to 1980 were equal to 2.35 t/ha, whereas the mean weighted grain yield in the Krasnoyarsk region for the same period was about 1.17 t/ha [12]. Therefore, we used both the reports from strain-testing stations and other published materials that provide information on the VM and crop yields from well fertilized plots (Table 4) and statistical data that give us averaged values [11].

All agrocenoses are characterized by two values of the reserves of VM: before and after the harvest. The reserves of C_{VM} in grain-producing agrocenoses depend on the fate of straw residues: they are much lower when straw is removed from the fields. For instance, the pool of C_{VM} on well fertilized wheat croplands before the harvest reaches 598 g/m^2, whereas after the harvest and straw removal it decreases down to 342 g/m^2. The main part of this pool (60–70%) is represented by dead plant remains of the preceding year.

Wheat yields ranging from 0.9 to 2.5 t/ha correspond to the reserves of C_{VM} varying from 370 to 600 g/m^2 (before harvesting); for barley yields of 0.8 to 3.2 t/ha, the reserves of C_{VM} vary from 340 to 700 g/m^2; for oats, these values constitute 1.3–2.9 t/ha and 370–650 g/m^2, respectively. The reserves of C_{VM} in the agrocenoses with wheat and oats are rather close to one another upon similar yields. Maximum reserves of C_{VM} are typical of barley agrocenoses developing on well fertilized plots (Table 4). The removal of grain products leads to a decrease in the reserves of C_{VM} to 310–570 g/m^2 for barley and oats; in wheat agrocenoses with removed grain, the C_{VM} content does not exceed 500 g/m^2. When the straw is also removed, the C_{VM} content in wheat agrocenoses ranges from 230 to 340 g/m^2; in the agrocenoses with oats, the remaining part of C_{VM} is minimal: 200–250 g/m^2. The reserves of C_{VM} in grain agrocenoses before and after harvesting depend on the particular proportions between the biomass of grain, straw, postharvest residues, and roots. These proportions depend on character of crop, regional peculiarities, and the degree of soil fertilization. For instance, the ratio of grain to straw (expressed in the organic carbon contents) in the steppe zone of Western Siberia constitutes 0.46 for wheat, 0.43 for barley, and 0.31 for oats in conditions of unfertilized plots; corresponding values for fertilized plots are 0.46, 0.47, and 0.50, respectively.

The effect of fertilizers on the contents of C_{VM} in wheat agrocenoses decreases from western to Eastern Siberia; this effect is mainly seen in agrocenoses of the steppe zone. For instance, application of fertilizers increases the reserves of C_{VM} in wheat agrocenoses of the steppe zone of Western Siberia (before harvesting) by 45% in comparison with unfertilized agrocenoses; in the forest-steppe zone of Eastern Siberia, this increase is much lower (22%). The removal of grain and straw from the fields makes regional differences less pronounced. In this case, the effect of fertilizers on the reserves of C_{VM} is assessed at 35% (Western Siberia) and 28% (Eastern Siberia). In barley agrocenoses, the effect of fertilizers on the accumulation of C_{VM} decreases from eastern to Western Siberia (i.e., has an opposite trend), though the character of zonal differences is preserved. In the steppe zone of Eastern Siberia, the C_{VM} content in fertilized barley agrocenoses before harvesting is 62% higher than that in unfertilized barley agrocenoses; in the forest-steppe zone of Western Siberia, this difference does not exceed 21%. After harvesting, fertilized plots in these two regions remain richer in C_{VM} by 35 and 15%, respectively. Similar regularities are observed for the agrocenoses with oats. The C_{VM} content in these agrocenoses before harvesting is 62% higher on fertilized plots in Eastern Siberia and just 24% higher in Western Siberia (if compared with unfertilized plots). Considerable difference between fertilized and unfertilized plots is also observed after the removal of grain (52 and 22% for eastern and Western Siberia, respectively); however, when both grain and straw are removed, this difference becomes less pronounced (23 and 17%, respectively).

This analysis is based on the statistical treatment of a great body of published data that mainly concern experimental farms and strain-testing stations. If we analyze data on average crop yields that are much lower (1.2–1.3 t/ha in Western Siberia), the reserves of C_{VM} before harvesting can be assessed at 400–420 g/m^2. After harvesting, the amount of crop residues getting into the soil decreases to 190–200 g C/m^2 per year; if the straw is also removed, the input of crop residues into the soil is assessed at 80–90 g C/m^2 per year. In Central Siberia, average yields of grain crops vary from 0.8 to 1.2 t/ha. The reserves of C_{VM} before harvesting are lower than those in Western Siberia and constitute about 310–320 g/m^2. The input of crop remains (together with straw) into the soil is assessed at 180 g C/m^2 per year; in the case of straw removal, it decreases to 80 g C/m^2 per year. Even lower yields are obtained in Eastern Siberia (0.6–1.2 t/ha). Correspondingly, the reserves of C_{VM} before harvesting range from 290 to 350 g/m^2. The input of plant remains (together with straw) into the soil after harvesting reduces to 130–190 g C/m^2 and, in the case of straw removal, does not exceed 70–80 g C/m^2 per year. For the whole territory of Siberia, the reserves of C_{VM} in grain agrocenoses before harvesting are assessed at 290–420 g/m^2, and the annual input of plant remains (together with straw) into the soil reaches 130–200 g C/m^2. Upon the removal of straw, annual supply of soil with plant remains decreases to 70–90 g C/m^2.

In fodder agrocenoses (corn and annual and perennial herbs), the reserves of C_{VM} range from 400 to 700 g/m^2 before harvesting and from 220 to 450 g/m^2 after harvesting. The reserves of C_{VM} in agrocenoses of the steppe and forest-steppe zones decrease by 1.4 times while moving from the west to the east of Siberia. The substitution of grain agrocenoses for virgin herbaceous eco-

Table 3. The reserves of C_{VM} in herbaceous ecosystems of Siberia

Ecosystem	Western Siberia		Central Siberia		Eastern Siberia	
	n	g/m^2	*n*	g/m^2	*n*	g/m^2
Flood-plain meadows						
Virgin	4	1440	5	1138	1	559
Mowed	4	1255	5	1195	1	752
Pasture	–	–	1	1014	1	992
Mesophytic meadows						
Virgin	2	1155	12	1075	–	–
Mowed	7	796	2	118	–	–
Pasture	3	713	9	699	–	–
Meadow steppes						
Virgin	6	1018	5	979	–	–
Mowed	19	974	4	1093	–	–
Pasture	5	877	3	1725	2	1324
True steppes						
Virgin	2	983	5	1417	2	620
Mowed	6	1104	–	–	–	–
Pasture	5	602	16	1118	10	1040
Dry steppes						
Virgin	–	–	5	776	–	–
Pasture	–	–	16	820	5	965

n denotes the number of studied ecosystems; dashes denote the absence of data.

Table 4. Crop yields (dry matter) and the reserves of vegetative matter (g C/m^2) in the soil layer of 0–30 cm under cereal agrocenoses

Region, natural zone	Grain yield, t/ha	Vegetative matter					
		before harvesting		after harvesting and the removal of			
				grain		grain and straw	
		1	2	1	2	1	2
Wheat							
Western Siberia							
Forest-steppe	1.6	452	598	382	501	259	342
Steppe	1.3	416	518	359	501	253	342
Central Siberia							
Forest-steppe	1.6	458	573	388	485	227	291
Steppe	1.4	435	599	373	502	227	291
Eastern Siberia							
Forest-steppe	1.5	447	548	381	469	227	290
Steppe	0.9	372	472	332	419	226	289
Barley							
Western Siberia							
Forest-steppe	2.0	523	633	435	519	241	277
Steppe	2.6	599	710	485	569	243	278
Central Siberia							
Forest-steppe	1.4	417	519	356	444	210	274
Steppe	1.7	458	658	381	535	211	277
Eastern Siberia							
Forest-steppe	0.8	341	467	306	410	209	273
Steppe	0.9	355	577	315	485	209	282
Oats							
Western Siberia							
Forest-steppe	2.1	504	625	412	502	210	246
Steppe	2.2	507	653	411	521	202	246
Central Siberia							
Forest-steppe	1.1	368	473	320	403	199	242
Steppe	1.7	446	564	371	463	201	245
Eastern Siberia							
Forest-steppe	1.4	408	642	346	555	200	244
Steppe	1.3	394	639	337	512	200	246

(1) Unfertilized plots; (2) fertilized plots (N > 30 kg/ha).

systems leads to a two- to threefold decrease in the pool of C_{VM}.

The Reserves of Microbial Biomass

The pool of microbial biomass (MB) represents a very dynamic link in the global carbon turnover. The dynamics of MB was studied in a chernozemic-meadow soil of a mesophytic meadow in the Krasnoyarsk region. It was shown that the pool of MB in this soil is characterized by considerable seasonal variations; at the same time, it is subjected to long-term fluctuations that manifest themselves as definite trends toward a decrease or increase in the MB for several years [19]. As a result of these variations, the maximum pool of MB in a given soil can be 3.6 times higher than its minimum pool (from 40 to 160 mg C/100 g soil). Changes in the pool of MB depend on several factors,

Table 5. The reserves of microbial biomass in the soil layer of 0–20 cm under natural ecosystems and agrocenoses

Land use	Western Siberia		Central and Eastern Siberia	
	n	MB, g/m^2	*n*	MB, g/m^2
Flood-plain meadows				
Virgin	4	531 ± 25.1	–	No data
Mowed	3	375 ± 79.6	–	No data
Forests and mesophytic meadows on gray forest soils				
Virgin	1	272	–	No data
Mowed	3	227 ± 24.5	–	No data
Pasturing, m.l.	3	171 ± 26.1	–	No data
Agrocenoses	7	62 ± 12.7	1	90
Mesophytic meadows on meadow-chernozemic and meadow soils				
Virgin	–	No data	–	No data
Mowed	3	254 ± 47.6	1	330
Pasturing, m.l.	–	No data	2	237
Agrocenoses	–	No data	1	96
Meadow steppes on leached chernozems				
Virgin	2	322	–	No data
Mowed	6	367 ± 48.4	–	No data
Pasturing, m.l.	1	329	–	No data
Agrocenoses	8	128 ± 47	–	No data
Dry steppes on southern chernozems				
Virgin	1	142	1	153
Mowed	–	No data	–	No data
Pasturing, m.l.	1	153	1	258
Pasturing, h.l.	–	No data	1	93
Agrocenoses	2	118	–	No data
Dry steppes on chestnut soils				
Virgin	–	No data	3	111 ± 11.5
Pasture:				
reserved	–	No data	1	56
winter	–	No data	5	65 ± 17
summer	–	No data	1	53
summer, m.l.	–	No data	1	68
Agrocenoses	–	No data	1	139

Dashes denote that these particular ecosystems were not studied; *n*, the number of studied ecosystems. Pasturing loads: reserved (no pasturing in recent years); l.l., low load; m.l., moderate load; h.l., high load.

including the availability of energy sources for microorganisms (organic matter), soil temperature, soil water content, and very complex trophic interactions between soil microflora and the other components of soil biota. The dynamic character of this pool makes it difficult to judge the reserves of microbial biomass in different ecosystems on the basis of one-time determinations, though these determinations may be sufficient for some general conclusions about changes in the microbial biomass in dependence on climatic conditions and land-management practices. Reliable quantitative data on the reserves of MB can only be obtained on the basis of long-term investigations into the dynamics of this component of soil organic matter.

Table 5 summarizes data on the microbial biomass in the soils of 76 Siberian ecosystems. These data can be used for revealing some general tendencies in the development of microbial biomass in different ecosystems. The amount of organic carbon bound in the microbial biomass (C_{MB}) of different ecosystems within the soil layer of

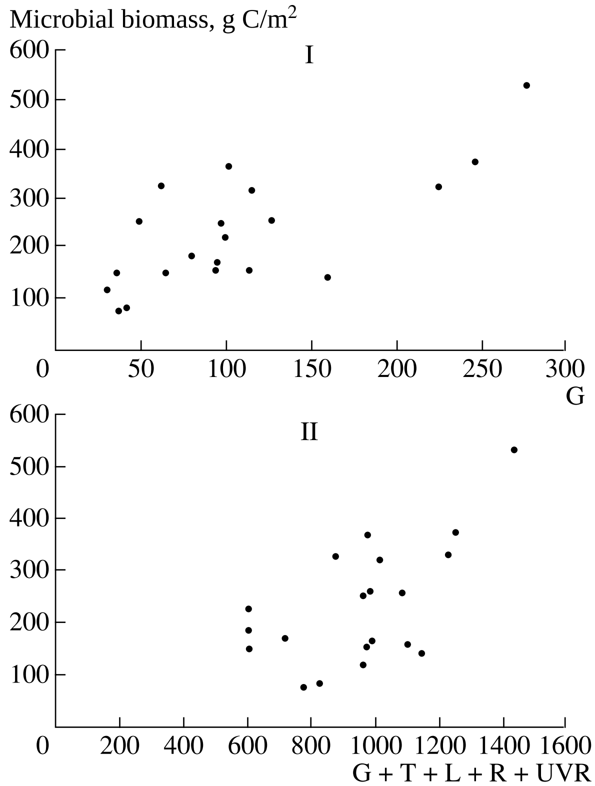

Fig. 1. The relationships between the reserves of microbial biomass (MB) and (I) green phytomass (G) and (II) total vegetative matter (G + T + L + R + UVR). Carbon reserves are given in g C/m^2; carbon reserves in roots and underground vegetative remains (R and UVR) are calculated for a soil layer of 0–20 cm. Correlation coefficient for MB and G equals 0.73; correlation coefficient for MB and VM equals 0.60. Explanations in the text.

0–20 cm varies from 50 to 530 g C/m^2, i.e., by an order of magnitude. This variation is three times higher than seasonal and long-term variations in the pools of MB in particular ecosystems. This fact allows us to analyze spatial regularities in the distribution of MB by the soils of different natural zones and ecosystems.

In Western Siberia, maximum reserves of MB are observed in the soils of flood-plain meadows without mowing. Regular mowing decreases the pool of MB in these soils by 1.5 times. The pool of MB in gray forest soils of the southern taiga zone in Western Siberia is twice as low as that in flood-plain meadow soils; it also depends on the character of phytocenoses and decreases in the following sequence: forest cenoses > hayfields > pastures > agrocenoses (croplands on gray forest soils). In meadow-chernozemic and meadow soils of mesophytic meadows in central and Eastern Siberia, the pool of MB is generally higher than that in gray forest soils. A regular decrease in the microbial biomass is observed upon the conversion of hayfields into plowed croplands.

The content of microbial biomass increases again in leached chernozems in the forest-steppe zone of Western Siberia. The soils of virgin, mowed, and pastured herbaceous ecosystems contain approximately equal amounts of microbial biomass; in agrocenoses, it decreases by 2.5 times. Herbaceous ecosystems in the forest-steppe zone of central and Eastern Siberia contain lower amounts of microbial biomass; no decrease in the MB content is observed in agrocenoses. In true steppes of Western Siberia with ordinary chernozems, a tendency toward a decrease in the MB content is observed upon their agricultural use. The MB contents in agrocenoses of the steppe and forest-steppe zones are similar. In southern chernozems of dry steppes, the reserves of MB are reduced by 1.5 times in comparison with those in ordinary chernozems. Maximum values are observed in the soils of pastures with moderate pasturing loads. Minimum values are typical of the soils of pastures with heavy pasturing loads and of the soils of agrocenoses.

Chestnut soils of dry steppes in Central Siberia contain the least amount of microbial biomass (68 g/m^2) among the studied ecosystems. The effect of pasturing loads on them is not pronounced: the soils of pastures contain about 67 g/m^2 of MB, whereas the soils of former pastures converted into reserved plots three years ago and having the grass cover similar to that on virgin plots contain just 56 g/m^2 of MB. It should be noted that these studies were conducted in the Tuva republic in the years with average climatic conditions. In these years, the full range of values for the MB density in the dry steppe zone of Tuva was from 53 to 102 g/m^2 [23]. In wet years, the MB content in these soils increases twofold.

The correlation coefficient between the MB content and the contents of all the subfractions of the VM is positive. However, this correlation is very weak and statistically insignificant for live roots (0.13), aboveground dead phytomass (0.32), and underground dead phytomass (0.42). The relationships between the MB and green phytomass and the MB and VM (green phytomass + twigs + litter + live roots + underground vegetation remains; G + T + L + R + UVR) are quite evident and statistically significant (Fig. 1). Positive correlation between MB and G was also revealed by Panikov *et al.* [9]. However, we believe that this correlation is not related to direct genetic relationship between these pools of organic matter; it is probable that both of them are closely connected with some other controlling factor, e.g., with moisture conditions. The correlation between MB and VM may explained by the role of VM as an energy supply for MB. The larger the pool of VM, the higher the mass of microorganisms consuming and transforming the vegetative matter.

Thus, the tendencies revealed in the behavior of MB demonstrate the effect of different factors: (a) climate (an increase in climatic humidity favors the development of MB); (b) energy source, i.e., vegetative matter; and (c) the character of land use (agrocenoses and pastures subjected to heavy loads in the zones of southern taiga, forest-steppe, and steppe are characterized by a considerable decrease in the pool of MB; in the dry

Table 6. The reserves of organic carbon in microbial biomass, soil layer of 0–20 cm

Ecosystem	Total MB, C_{MB}	Carbon of micromycetes	
	g/m^2		% of C_{MB}
Herbaceous ecosystems			
Meadow-chernozemic soil, reserved steppe meadow, CS	143	20	14
Leached chernozem, steppe meadow, idle land, WS	286	10	3
Leached chernozem, meadow steppe, virgin plot, WS	358	11	3
Leached chernozem, meadow steppe, CS	415	41	10
Leached chernozem, meadow steppe, ES	224	25	11
Southern chernozem, steppe, pasture with high loads, WS	154	12	8
Southern chernozem, steppe, pasture with moderate loads, WS	205	13	6
Chestnut soil, dry steppe, summer pasture, CS	120	14	12
Chestnut soil, dry steppe, winter pasture, CS	65	13	20
Cryoarid chestnut soil, dry steppe, pasture, ES	118	28	24
Average for herbaceous ecosystems	208	19	9
Agrocenoses			
Soddy-podzolic soil, oats, WS	111	9	8
Leached chernozem, corn, WS	175	16	9
Leached chernozem, wheat, CS	139	20	14
Leached chernozem, clean fallow, CS	251	18	7
Leached chernozem, green fallow, CS	251	20	8
Leached chernozem, oats, CS	185	25	14
Ordinary chernozem, corn, WS	249	13	5
Solonetzic ordinary chernozem, corn, WS	150	14	9
Southern chernozem, oats, WS	118	15	13
Southern chernozem, wheat, WS	117	18	15
Cryoarid chestnut soil, clean fallow, ES	128	22	17
Average for agrocenoses	170	17	10

WS, CS, and ES are abbreviations for Western, Central, and Eastern Siberia, respectively.

steppe zone, where agrocenoses occupy better moistened areas, the reserves of MB in them may be even higher than in the soils of pastures).

The Reserves of Fungal Biomass

In the soils under forests, fungal biomass may constitute up to 65% of the total biomass of soil microorganisms. In herbaceous ecosystems, the fungal biomass content varies from 11 to 41 g/m^2 constituting from 3 to 24% of the MB. Therefore, the pool of fungal biomass (FB) is more stable than its relative contribution to the total pool of MB. The minimum contribution of FB to MB (about 3%) is observed in the soils of meadow steppes; the maximum contribution (12 to 24%) is typical of the soils of pastures in the dry steppe zone. An increase in the share of FB in MB in arid soils is mainly due to a very significant decrease in the density of bacterial population (Table 6).

In agrocenoses, the FB pool varies from 9 to 25 g/m^2, and its contribution to the total pool of MB changes from 7 to 17%. There is no definite effect of climate on the pool of FB in agrocenoses. Regular soil tillage and other treatments in agrocenoses level environmental conditions, which is manifested by a more stable proportion between bacterial and fungal biomass. At the same time, a weak tendency for a decrease in the FB content in agrocenoses is observed. The contribution of spores to the total FB ranges from 10 (cryoarid chestnut soil) to 60% (solonetzic ordinary chernozem). In agrocenoses, the relative content of fungal spores is usually higher than that in natural herbaceous ecosystems. Pasturing loads may lead to a considerable decrease in the content of fungal spores. In general, it can be assumed that the main part of microbial biomass in human-modified soils of herbaceous ecosystems is represented by the bacterial community.

Table 7. The reserves of organic carbon (million tons C) in the vegetative matter of initial ecosystems and modern agrocenoses

Ecosystem	Southern taiga	Forest-Steppe	Steppe	Mountainous regions	River valleys	Total
Former vegetation (reconstructed)						
Coniferous taiga	88.30	–	–	–	–	88.30
Mixed forests	18.10	–	–	–	–	18.10
Deciduous hardwood forests	68.80	185.61	0.40	–	–	254.81
Riparian forests	–	–	–	–	0.71	0.71
Mesophytic meadows	0.20	3.59	–	–	–	3.79
Meadow steppes	–	93.71	8.31	–	0.19	102.21
True steppes	–	–	48.90	–	–	48.90
Dry steppes	–	–	0.89	–	–	0.89
Solonetzic and solonchakous steppes and meadows	–	5.89	2.50	–	–	8.39
Mountainous meadows and steppes	–	–	–	0.60	–	0.60
Herbaceous mires	–	0.31	–	–	–	0.31
On the total	175.40	289.11	61.00	0.60	0.90	527.01
Agrocenoses						
Cereals and leguminous crops	3.25	34.83	11.27	0.20	0.27	49.82
Potatoes and vegetables	0.03	0.86	0.21	–	0.01	1.11
Industrial crops	0.02	0.38	0.36	–	–	0.76
Fodder crops	3.07	20.75	6.47	0.12	0.15	30.56
Fallow fields	0.21	2.81	1.51	–	0.01	4.54
On the total	6.58	59.63	19.82	0.32	0.44	86.79

Dashes denote the absence of a given type of ecosystem in the corresponding zonal (or azonal) landscape.

Table 8. The reserves and losses (million tons) of the carbon of vegetative matter and soil organic matter related to soil plowing in the south of Western Siberia (by 1990)

Landscape regions	Carbon reserves				Carbon losses from:	
	former vegetation		agrocenoses		VM	SOM
	VM	SOM	VM	SOM		
Southern taiga	175.4	216	6.6	179	168.8	37
Forest-Steppe	289.1	2590	59.6	1822	229.5	768
Steppe	61.0	1116	19.8	812	41.2	304
Mountainous landscapes	0.6	15	0.3	11	0.3	4
River valleys	0.9	17	0.4	10	0.5	7
Total	527.0	3954	86.7	2834	440.3	1120

Changes in the Carbon Budget

The transformation of natural ecosystems into agrocenoses is accompanied by a decrease in the reserves of vegetative matter and soil organic matter (SOM), net primary production (NPP), and annual input of vegetative remains into the soil. In 1990, the area of agrocenoses in Western Siberia reached 19 500 million hectares. These agrocenoses had replaced diverse natural ecosystems: from coniferous forests to dry steppes. In the last 150 years, about 3.2 million ha of forest lands, 10 million ha of meadow steppes, 5 million ha of true steppes and dry steppes, and 0.8 million ha of meadows have been plowed and converted into croplands. At present, grain and leguminous crops are grown over about 11.1 million ha; fodder crops, on 5.5 million ha; industrial crops, on 0.4 million ha; and fallow fields occupy about 2.3 million ha [16]. On the basis of data on the reserves of organic carbon in natural forests

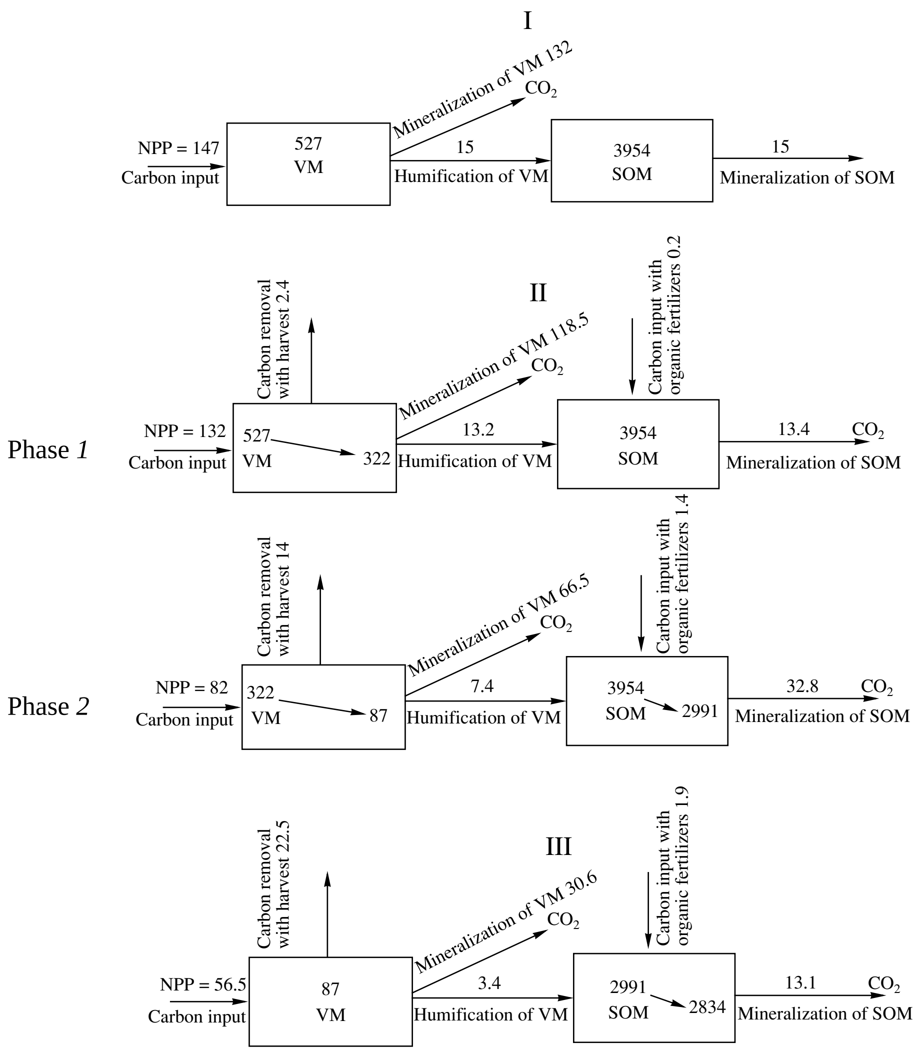

Fig. 2. Changes in the carbon budget of the territory occupied by agrocenoses within the last 200 years, Western Siberia. Carbon reserves are shown in rectangles; arrows inside them indicate changes in these reserves; and arrows between rectangles, carbon fluxes (all values in million tons of organic carbon). Stages of transformation: (I) initial stationary state of carbon turnover (before 1800); (II) transitional stages: (II-*1*) phase *1* (partial transformation of initial virgin cenoses into agrocenoses, 1800–1930) and (II-*2*) phase *2* (transition from partly to completely transformed agrocenoses, 1930–1970); and (III) secondary quasiequilibrium state of carbon turnover in agrocenoses (1970–1990).

(including the carbon of dead stands and litter) collected by Bazilevich [2] and our materials on carbon contents in natural herbaceous ecosystems and agrocenoses, we can calculate the total amounts of organic carbon in modern agrocenoses and in the ecosystems that existed in place of these agrocenoses in the preagricultural period (Table 7). The modern pool of VM is six times lower than in the past (Table 8). In the last 200 years, the loss of C_{VM} from natural cenoses converted into croplands has reached 440×10^6 t. The highest losses are typical of the southern taiga, where forests were replaced by agrocenoses, and of the forest-steppe zone. Along with the loss of VM, the reserves of soil organic carbon have been also reduced owing to a more rapid mineralization of soil organic matter in agrocenoses. The loss of soil organic carbon is assessed at 1120×10^6 t (Table 8). Soils of the forest-steppe zone have lost about 30% of the initial organic carbon; and soils of the steppe zone, about 27%. The total loss of organic carbon (VM + soil organic matter) constitutes about 1560.3×10^6 t (Table 8).

The loss of organic carbon from local ecosystems owing to their agricultural development has been observed since the beginning of the 19th century. By 1860, the area of croplands reached about 2240000 ha, or 10% of the modern area of plowed soils. Forest cuts and the development of forest and steppe lands resulted in the loss of vegetative matter. However, the reserves of soil organic matter were relatively stable. This was conditioned by the application of traditional Siberian crop rotation systems with long-term fallowing: six years under crops, nine years under green fallow, and two years under black fallow. Long-term fallowing led to the replenishment of humus reserves in soils [7]. In the 1930s, after collectivization of farms, this system was replaced by crop rotation systems with short-term fallowing or without fallowing at all. Annual losses of soil organic carbon in the first decade of continuous plowing reach 420 g/m^2. This carbon is mainly lost from the reserves of labile soil carbon stored in detritus, microbial biomass, and nonspecific organic compounds). Afterwards, the rate of losses decreases down to 8 g/m^2 per year. There were two periods with especially active losses of soil organic carbon: in the 1930s and 1940s (after the collectivization) and from 1953 to 1960 (after the wide-scale plowing of virgin lands) [8, 18]. The losses of vegetative matter have been increasing since the 1860s owing to a progressive increase in the area of agrocenoses. A decrease in phytomass reserves and lower yielding capacity of agrocenoses (as compared to that in natural herbaceous cenoses) leads to some decrease in the net primary production (NPP) over the territory [16]. We have calculated NPP values and the removal of organic carbon with harvests for different stages of the transformation of natural cenoses into agrocenoses (Fig. 2).

Stage I is characterized by the stationary regime of the biological turnover of carbon in natural ecosystems. The reserves of VM and SOM remain stable, and NPP can be calculated as the difference between the gross primary production and the mineralization of VM and SOM.

Stage II is characterized by the replacement of natural vegetation by crops. It can be subdivided into two phases. Phase *1* corresponds to crop rotation systems with long-term fallow (from 1860 to 1930). Phase *2* corresponds to crop rotation systems with continuous plowing (from 1930 to 1970). Phase *1* is characterized by a decrease in the VM content upon a relatively stable content of SOM. Mineralization of VM and SOM is somewhat lower than the NPP. The CO_2 release from agrocenoses is somewhat lower than that in natural cenoses owing to the removal of a part of organic carbon with harvests. Phase *2* is characterized by a sharp decrease in the reserves of both VM and SOM. Mineralization of the remaining part of VM and SOM and the removal of organic carbon with harvests are 35% higher than the input of organic carbon into agrocenoses (i.e., NPP + organic fertilizers). This results in a general depletion of the organic carbon pool and additional emission of carbon dioxide into the atmosphere owing to a rapid mineralization of the labile part of SOM.

Stage III is characterized by the relatively stable total area of agrocenoses (from the 1970s to the 1990s). The last two decades were marked by a quasistationary regime of carbon turnover in agrocenoses; neither the area nor the NPP of these agrocenoses have changed. The reserves of VM in them remain stable (though at a low level); the decrease in the reserves of SOM (owing to mineralization and erosion losses) is not very significant. In total, the loss of carbon from agrocenoses is just 12% higher than the input of organic carbon in them.

Starting from the 1990s, a tendency toward a decrease in the area of croplands has been observed. Abandoned plowlands are overgrown by natural vegetation. At present, we do not have quantitative estimates of the effect of this process on the carbon cycling. However, the general tendency is quite clear: a rapid growth in the reserves of vegetative matter and a slow growth in the reserves of soil organic matter should take place.

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