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SOIL PHYSICS

Relationship of Methane Consumption with the Respiration of Soil and Grass–Moss Layers in Forest Ecosystems of the Southern Taiga in Western Siberia

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Abstract—The consumption of methane by some soils in the southern taiga of Western Siberia was studied by the static chamber method in the summer of 2013. The median of the specific CH_4 flux through the soil was –0.05 mg C/(m^2 h) for the entire set of measurements (the negative flux indicates the consumption of methane by the soil). A statistically significant ($R^2 = 0.81$) linear relationship has been found between the specific CH_4 flux to the soil and the total respiration of the soil and the grass–moss layers in the studied forest ecosystems. The quantitative theoretical explanation of this relationship is based on the plant-associated and free methanotrophy.

Keywords: rhizospheric methanotrophs, total soil and plant respiration, greenhouse gases, Fluvisol, Luvisol, Gleysol

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INTRODUCTION

The accumulation of greenhouse gases in the atmosphere is one of the current global environmental problems [31]. The major contributions to the greenhouse effect are made by CO_2 and CH_4: 60 and 15%, respectively [43]. For understanding the natural changes, the inventory of sources and sinks, the assessment of their intensities and dynamics, and the investigation of their functioning mechanisms are necessary [31].

As for the study of specific CH_4 fluxes, the most numerous measurements were performed in Western Siberia, but the studies were somewhat unbalanced: only the emission of methane from natural bogs and lakes was studied [11, 29, 30, 42]. Single measurements of methane consumption, if any, were occasional: the emission of CH_4 was expected to be revealed in the methane-generating ecosystems, but its consumption was rarely observed [9, 12, 26]. In European Russia, both the emission of methane from the soils of forest, bogs, and areas under agricultural use, as well as their consumption, were studied [13, 15, 16]. The comparison of specific fluxes (in mass units of the gas released from the soil surface in unit time) shows that the bogs as methane sources significantly exceed any soil sinks of this gas. However, the total bog area is significantly smaller than the area of CH_4 sinks (i.e., soils of fields, forests, etc.), so the latter cannot be ignored; on the contrary, they should be thoroughly studied to obtain an accurate balance. Earlier theoretical calculations using five different procedures showed that the soils of Russia consume 3.6 Mt of methane annually [2], while its emission is estimated by different authors at 7.5 to 23.5 Mt/year [7, 19, 46].

Regrettably, the assessment of methane consumption by the soil is a more difficult technical problem, because the CH_4 concentration should be measured in the range from the atmospheric to the null level in this case, while the measurements of methane emission include the analysis of concentrations exceeding the atmospheric level (frequently by several times). Therefore, along with the direct measurements of methane consumption, of special importance is the search of correlations between the CH_4 consumption rate and some parameters easier to measure.

Studies of oligotrophic bogs in Western Siberia revealed only a loose reliable correlation between the specific CH_4 flux and the emission of CO_2 due to the total respiration of the soil and the grass–moss layers [4]. In theoretical terms, a stronger correlation between these parameters could be expected in less wet soils. In addition, the significant role of CO_2 in the greenhouse effect attracts the attention of researchers to measurements of its specific fluxes [10, 14, 28, 39].

The general goal of recent studies is to close these gaps in studying the role of biogeocenoses in the cycle of methane as a greenhouse gas; therefore, this work was aimed at measuring the rate of methane consumption by forest soils in the southern taiga of Western Siberia and revealing (if possible) the quantitative relationship between the consumption of methane and the respiration of the soil and the grass–moss layers.

OBJECTS AND METHODS

The measurements were conducted on several key plots near the settlement of Plotnikovo in the Bakchar district of Tomsk oblast, the southern taiga subzone of Western Siberia, in the summer of 2013. The sampling sites were selected in order to reflect the natural diversity of forest communities in the area studied. The detailed description of the sampling sites is given in Table 1.

The specific CH_4 fluxes were measured by the static chamber method [13, 15, 32] described earlier [32]. A stainless steel support (37×37 or 40×40 cm^2 in cross-section and 15 cm in height) was inserted into the soil to a depth of 10–15 cm no earlier than 15 min before the measurements, in order for the disturbances of the methane concentration profile in the soil caused by the insertion of the support to be leveled. Then, a Plexiglas chamber (parallelepiped $30 \times 30 \times 40$ cm^3 in size, without the lower face) was installed on the support, and the contact between the chamber and the support was sealed with a hydraulic lock (water was filled in the support grooves so that the contact between the lower part of the chamber and the support was immersed in water to a depth of at least 1 cm). A rubber cork, through which a metallic tube with a fitted rubber tube was passed, was then inserted into the hole in the upper face of the chamber. An SFM syringe for gas sampling was connected to the rubber tube. The sampling was performed in time moments $t_0 = 0$, t_1, t_2, and t_3 with equal intervals. The time of exposure ($t_3 - t_0$) was 60 min.

The syringes with the samples were kept in soil solution to prevent leakage of methane, which is poorly soluble in salt water. The gas concentration in the samples was measured on a modified KhPM-4 chromatograph (Khromatograf, Moscow, USSR) equipped with a gas line and a flame ionization detector from an LKhM-80 chromatograph (Khromatograf, Moscow, USSR). A steel column (1 m long, 2.5 mm in diameter) packed with Sovpol (80–100 mesh) was used. The measurements were performed at 40°C; hydrogen was used as a carrier gas (flow rate 5 mL/min); the injector loop volume was 0.5 mL. The sample volume was 3 mL. Standard methane–air mixtures with CH_4 concentrations of 1.99, 5.00, and 9.84 ppmv (National Institute for Environmental Studies, Japan) were used for calibration; the standard concentration accuracy was ±0.01 ppvm.

Air samples for the analysis of carbon dioxide concentrations were taken from light-proof chambers in an analogous way, simultaneously with the samples for methane determination, but the time intervals between each of the four sampling events were 3 min to prevent the excess increase in CO_2 concentration. Plants were not removed during the measurements. Carbon dioxide–air mixtures with CO_2 concentrations of 357 ± 5 and 708 ± 10 ppmv (VNIIMEM, St. Petersburg, Russia) were used for calibration.

The concentration of carbon dioxide was analyzed no later than several hours after sampling on a DX-6100 infrared gas analyzer (RMT Ltd., Moscow, Russia).

Soil and air temperatures were measured with Thermochron iButton DS1921G temperature loggers (Dallas Semiconductor, USA). Vegetation descriptions were performed according to [3]. Soil names are given in accordance with the current classification of Russian soils [6] and the international WRB soil classification [45].

Specific fluxes were calculated by the regression method in the time–concentration coordinates using linear regression for the emission of CO_2 and nonlinear regression for the consumption of CH_4 as described earlier [1]. The statistical processing of data (including the comparison of the means using the Wilcoxon test, as well as linear and nonlinear one-parameter regressions) was performed using interactive MATLAB environment (v. 7.0, MathWorks, USA).

RESULTS AND DISCUSSION

The results of individual measurements of specific CO_2 fluxes, as well as air and soil temperatures at the measurement moments, are given in Table 2. Analogous data for specific methane fluxes are given in Table 3. The positive fluxes denote the emission of methane and carbon dioxide to the atmosphere, and the negative fluxes correspond to their consumption. Some statistical characteristics of the distributions of the measured specific CH_4 and CO_2 fluxes and other integral parameters are given in Table 4. The median of specific CH_4 fluxes was –0.05 mg C/(m^2 h) for the entire set of measurements, which indicated the consumption of methane by the soil. These results well agree with the data obtained for other forest ecosystems in the zones of broad-leaved forests and southern taiga (Table 5).

A statistically significant correlation ($n = 8$, $R^2 = 0.81$) was found between the median of CH_4 specific

Table 1. Characterization of the objects of study

Measurement point (data)	Coordinates	Forest characterization	Dominant plant species*	Soil type (WRB)	Organic horizon depth, cm	Some soil properties (at 0–10 cm, without forest litter or moss)		
						pH_{water}	C_{org}, %	density, g/cm^3
T.Plo.For.1.25 (24.06.2013) T.Plo.For.1.26 (27.06.2013)	56.8617° N, 83.077° E, 56.8616° N, 83.0723° E	Overmoistened birch forest in the Iksa River floodplain	*Bet*, *Al*, *Cal*	alluvial clay-mucky gley soils (Gleyic Histic Fluvisols (Eutric, Siltic))	17	6.2	7.7	1.1
Plo.For.Iksa.R (18.07.2013 è 19.08.2013)	56.9621° N, 83.0700° E	Strongly moistened southern-taiga spruce forest	*Pic*, *Car*, *Bet*, *Sor*, *Mat*, *Ox*, *Sp*	Gleyic soddy-podzolic soils with a second humus horizon (Albic Stagnic Luvisol (Cutanic, Siltic))	12	5.3	2.5	1.2
Plo.For.Razr (10.08.2013)	56.9116° N, 83.0527° E	Thick grass–green moss cedar–fir forest	*Ab*, *Pin*, *Pr*, *Car*, *Ox*, *Mai*, *Eq*, *Gal* various mosses	Gleyic soddy-podzolic soils with a second humus horizon (Albic Luvisol (Cutanic, Siltic))	7	5.5	2.9	1.3
Plo.For.Razr2 (12.08.2013) Plo.For.Razr2.1 (12.08.2013)	56.9091° N, 83.0547° E, 56.9090° N, 83.0550° E	Polydominant small grass–sedge–sphagnum–green moss fir–spruce–cedar forest	*Pin*, *Pic*, *Ab*, *Bet*, *Sor*, *Ox*, *Mai*, *Sp*	Mucky-humus gley soils (Eutric Histic Gleysol (Clayic, Humic))	24	5.7	6.7	1.2
Birch.For (16.08.2013)	56.8766° N, 82.9042° E	Secondary young (40-year-old) forest	*Bet*, *Cal*, *Eq*	Soddy-mucky gley soils (Eutric Gleysol (Clayic, Humic))	29	5.8	8.3	1.1

* (*Bet*) *Betulapendula*; (*Cal*) *Calamagrostispurpurea*; (*Ab*) *Abies sibirica*; (*Al*) *Alnus glutinosa*; (*Ox*) *Oxalis acetosella*; (*Mai*) *Maianthemum bifolium*; (*Eq*) *Equisetum sylvaticum*; (*Gal*) *Galium palustre*; (*Sp*) *Sphagnum*; (*Pic*) *Picea obovata*; (*Pin*) *Pinus sibirica*; (*Pr*) *Prunuspadus*; (*Sor*) *Sorbus sibirica*; (*Car*) *Caragana arborescens*; (*Mat*) *Matteuccia struthiopteris*.

Table 2. Emission of CO_2 from taiga soils of Western Siberia, the Plotnikovo key plot

Temperature, °C					Specific CO_2 flux, mg C–CO_2/(m^2 h)	
air	soil, depth, cm				mean	S*
	0	5	10	15		
T. Plo.For. 1.25, birch forest						
18.7	16.6	13.4	11.8	11.8	50	8
18.7	16.6	13.4	11.8	11.8	29	7
12.2	13.2	12.7	11.5	11.9	77	14
12.2	13.2	12.7	11.5	11.9	104	6
12.2	13.2	12.7	11.5	11.9	90	10
T. Plo.For. 1.26 (measurement date 27.06.2013) birch forest, southern taiga						
23.5	21.7	15.5	14.5	12.9	235	41
23.5	21.7	15.5	14.5	12.9	155	5
T. Plo.For. Razr cedar–fir forest						
24.1	20.2	18.5	18.0	18.0	1242	168
23.8	20.2	18.3	17.8	17.8	821	59
23.5	20.1	18.3	17.7	17.7	636	33
23.2	20.0	18.0	17.3	17.3	464	21
23.0	19.9	17.9	17.2	17.2	422	18
22.8	19.9	17.8	17.0	17.0	474	24
20.8	19.3	16.6	15.5	15.3	1145	37
20.5	19.2	16.5	15.3	15.0	1599	64
20.1	20.1	16.9	15.2	15.1	1311	83
22.4	19.7	17.6	16.7	16.7	448	12
22.2	19.7	17.4	16.5	16.5	538	47
21.9	19.6	17.3	16.4	16.4	534	30
21.6	19.5	17.1	16.1	16.1	1235	221
21.4	19.4	17.0	15.9	15.9	968	44
21.1	19.4	16.9	15.8	15.7	961	255
20.0	19.1	16.0	15.0	14.5	751	67
19.7	19.0	16.0	14.7	14.2	739	31
19.5	18.9	16.0	14.5	14.0	681	58
T. Plo.For.Razr2 fir–spruce–cedar forest						
21.0	21.5	16.6	14.5	14.3	525	41
21.0	21.5	16.1	14.5	14.0	585	72
21.0	21.1	16.0	14.5	14.0	292	40
22.3	21.9	16.0	14.5	14.0	411	8
23.4	22.4	16.0	14.5	14.0	384	20
22.6	22.5	16.0	14.8	14.0	383	27
22.5	22.5	16.0	15.0	14.0	344	9
23.1	22.9	16.0	15.0	14.0	639	81
22.8	22.5	16.0	15.0	14.0	583	29
T. Plo.For.Razr2.1 ir–spruce–cedar forest						
22.0	21.9	16.0	15.0	14.0	471	22
22.0	21.5	16.1	15.0	14.0	489	34
22.0	21.5	16.2	15.0	14.0	417	21
21.5	21.2	16.5	15.0	14.0	447	28
21.3	21.0	16.4	15.0	14.0	641	62
21.5	21.0	16.5	15.0	14.0	448	12
21.5	21.4	16.5	15.0	14.0	419	29
21.5	21.0	16.5	15.0	14.0	571	24
21.3	21.0	16.5	15.0	14.0	861	99
T. Birch.For birch forest						
18.5	18.7	15.5	14.5	14.0	196	24
18.5	18.7	15.5	14.5	14.0	310	14
18.5	18.7	15.5	14.5	14.0	452	30
18.5	18.7	15.5	14.5	14.0	278	23
18.1	18.0	15.5	14.5	14.0	672	51
18.0	17.9	15.5	14.5	14.0	755	37
18.0	17.9	15.5	14.5	14.0	583	26
17.1	16.9	15.5	14.5	14.0	384	69
16.6	16.4	15.5	14.5	14.0	745	32
16.5	16.1	15.5	14.5	14.0	546	26
14.9	15.3	15.5	14.5	14.0	1512	182
14.3	14.9	15.0	14.5	14.0	514	17
13.8	14.5	15.0	14.5	14.0	1409	174
13.4	14.1	15.0	14.5	14.0	1200	115
12.5	13.5	15.0	14.5	14.0	569	13
12.1	13.3	15.0	14.5	14.0	906	10
12.1	13.3	15.0	14.5	14.0	833	50
11.5	13.0	15.0	14.5	14.0	675	146
18.1	18.0	15.5	14.5	14.0	877	48
18.1	18.0	15.5	14.5	14.0	681	47
18.1	18.0	15.5	14.5	14.0	457	17
18.0	17.9	15.5	14.5	14.0	678	35
18.0	17.9	15.5	14.5	14.0	576	57
16.5	16.5	15.5	14.5	14.0	455	15
16.5	16.3	15.5	14.5	14.0	366	23
16.1	16.0	15.5	14.5	14.0	735	75
15.6	15.9	15.5	14.5	14.0	920	19
15.2	15.5	15.5	14.5	14.0	1550	179
12.5	13.5	15.0	14.5	14.0	296	32
12.5	13.5	15.0	14.5	14.0	326	18
12.5	13.5	15.0	14.5	14.0	272	40

Table 2. (Contd.)

Temperature, °C					Specific CO_2 flux, mg C–CO_2/(m^2 h)		Temperature, °C					Specific CO_2 flux, mg C–CO_2/(m^2 h)	
air	soil, depth, cm				mean	S*	air	soil, depth, cm				mean	S*
	0	5	10	15				0	5	10	15		
12.1	13.3	15.0	14.5	14.0	649	31	18.3	18.8	17.6	15.6	14.4	579	35
12.1	13.3	15.0	14.5	14.0	681	25	18.0	18.3	17.0	15.0	14.0	343	24
11.5	13.0	15.0	14.5	14.0	789	70	18.0	18.0	17.0	15.0	14.0	475	8
11.5	13.0	15.0	14.5	14.0	896	62	18.0	18.0	17.0	15.0	14.0	229	17
11.5	13.0	15.0	14.5	14.0	658	78	19.0	18.5	16.5	14.7	14.0	416	17
T. Plo.For.Iksa.R (measurement date 18.07.2013) spruce forest							19.0	18.5	16.5	14.7	14.0	335	9
23.6	21.6	16.0	15.6	15.2	291	7	18.8	18.5	16.5	14.8	14.0	422	133
23.6	21.6	16.0	15.6	15.2	265	8	18.5	18.1	16.5	14.7	14.0	465	29
23.6	21.6	16.0	15.6	15.2	266	9	18.5	18.0	16.5	14.8	14.0	517	68
23.6	21.6	16.0	15.6	15.2	452	15	18.6	18.5	16.5	14.8	14.0	390	23
23.2	21.2	15.9	15.5	15.0	346	20	19.0	18.5	16.5	14.7	14.0	364	37
23.2	21.2	15.9	15.5	15.0	367	79	19.0	18.5	16.5	14.8	14.0	387	37
21.7	20.1	15.5	15.0	14.9	352	28	18.8	18.5	16.5	14.8	14.0	300	56
21.7	20.1	15.5	15.0	14.9	400	8	18.5	18.3	16.5	14.9	14.0	307	15
21.4	20.0	15.5	15.0	14.8	451	87	18.0	18.0	16.6	15.0	14.0	420	8
21.4	20.0	15.5	15.0	14.8	422	12	18.4	18.0	16.5	15.0	14.0	391	14
23.0	21.0	15.5	15.0	15.0	345	12	19.0	18.5	16.5	14.8	14.0	356	20
23.0	21.0	15.5	15.0	15.0	191	41	18.5	18.5	16.5	14.9	14.0	303	50
23.2	21.0	15.5	15.0	15.0	376	88	18.8	18.5	16.5	14.9	14.0	344	10
23.2	21.0	15.5	15.0	15.0	288	53	18.5	18.0	16.5	14.9	14.0	367	11
22.0	20.5	15.5	15.0	15.0	426	56	18.0	18.0	16.5	14.8	14.0	331	29
22.0	20.5	15.5	15.0	15.0	408	18	18.0	18.0	16.5	14.8	14.0	367	6
21.0	19.7	15.5	15.0	15.0	518	33	18.8	18.4	16.5	14.8	14.0	421	94
21.0	19.7	15.5	15.0	15.0	495	24	18.5	18.0	16.5	14.9	14.0	357	20
20.5	19.5	15.5	15.0	15.0	481	121	18.1	18.0	16.5	14.8	14.0	292	11
20.5	19.5	15.5	15.0	15.0	254	49	17.9	17.8	16.5	14.9	14.0	295	100
T. Plo.For.Iksa.R (measurement date 19.08.2013) spruce forest							17.5	17.5	16.5	14.7	14.0	213	40
18.4	18.9	17.8	15.8	14.6	335	106	17.4	17.5	16.5	14.5	14.0	281	54

* (S) standard deviation.

flux (SF, mg C–CH_4/(m^2 h)) from the soil in each of the studied points and the median of the total respiration of soil and grass–moss layers (TR, mg C–CO_2/(m^2 h)):

$$\mathrm{SF\,CH_4} = a\,\mathrm{TR} + b, \qquad (1)$$

where $a = -(0.000157 \pm 0.000031)$ mg C–CH_4/mg C–CO_2; $b = 0.015 \pm 0.014$ mg C–CH_4/(m^2 h); and the standard error of the regression is 0.018 mg C–CH_4/(m^2 h) (figure). It can be seen that when the respiration rate of plants increases, the specific methane consumption rate also increases.

This relationship can be explained from the positions of two types of methanotrophy related to the activity of free-living methanotrophs [24, 34, 35] and plant-associated methanotrophs [23, 33, 38]. It should be noted that 33% of the total methane consumed by microorganisms is assimilated, and 60% is oxidized to carbon dioxide [8].

Methanotrophic bacteria are known to be permanently present in the phyllosphere and the rhizo-

Table 3. Methane emission from taiga forests of Western Siberia, the Plotnikovo key plot

Temperature, °C					CH_4 flux, mg $C{-}CH_4/(m^2$ h)	
air	soil, depth, cm				mean	*S*
	0	5	10	15		
T. Plo.For.1.25, birch forest						
18.7	16.6	13.4	11.8	11.8	–0.020	0.057
18.7	16.6	13.4	11.8	11.8	0.013	0.032
12.2	13.2	12.7	11.5	11.9	0.050	0.021
12.2	13.2	12.7	11.5	11.9	0.006	0.078
12.2	13.2	12.7	11.5	11.9	–0.012	0.469
12.2	13.2	12.7	11.5	11.9	–0.029	0.154
T. T.Plo.For.1.26 birch forest, southern taiga						
23.8	21.3	14.5	13.7	12.3	–0.040	0.113
23.8	21.3	14.5	13.7	12.3	–0.016	0.139
T. Plo.For.Razr cedar–fir forest						
23.5	20.1	18.2	17.6	17.6	–0.064	0.277
23.5	20.1	18.2	17.6	17.6	–0.151	0.045
21.9	19.6	17.3	16.4	16.4	–0.098	0.362
21.9	19.6	17.3	16.4	16.4	–0.085	0.086
20.4	19.2	16.4	15.2	14.9	–0.010	0.149
20.4	19.2	16.4	15.2	14.9	–0.149	0.101
Plo.For.Razr2 (on the right) and Razr2.1(on the left), fir–spruce–cedar forest						
21.4	21.5	16.1	14.5	14.0	–0.007	0.136
21.4	21.5	16.1	14.5	14.0	–0.055	0.094
22.7	22.5	16.0	14.9	14.0	–0.045	0.268
22.7	22.5	16.0	14.9	14.0	–0.027	0.058
21.8	21.5	16.2	15.0	14.0	–0.052	0.290
21.8	21.5	16.2	15.0	14.0	–0.090	0.225
T. Birch.For birch forest						
16.8	16.6	15.5	14.5	14.0	–0.113	1.362
16.8	16.6	15.5	14.5	14.0	–0.129	0.228
16.8	16.6	15.5	14.5	14.0	–0.122	0.035
15.6	15.8	15.5	14.5	14.0	–0.120	0.211
15.6	15.8	15.5	14.5	14.0	–0.095	0.097
15.6	15.8	15.5	14.5	14.0	–0.065	0.060
T. Plo.For.Iksa.R (measurement date 18.07.2013) spruce forest						
28.2	19.4	16.9	16.6	–	–0.54	0.30
28.7	20.8	19.0	17.5	–	0.07	0.09
31.7	23.6	20.4	19.7	–	0.16	0.07
30.7	22.5	20.0	19.5	–	–0.01	0.32
27.3	22.0	20.0	19.5	–	–0.16	1.01
–	22.0	21.0	19.5	–	–0.02	0.05
T. Plo.For.Iksa.R (measurement date 19.08.2013) spruce forest						
18.1	18.3	17.0	15.2	14.1	–0.037	0.261
18.3	18.2	16.6	14.9	14.0	0.000	0.200
18.7	18.3	16.5	14.8	14.0	–0.022	0.103
17.3	17.4	16.5	14.6	14.0	–0.264	0.338
17.3	17.4	16.5	14.6	14.0	–0.021	0.076
18.8	18.4	16.5	14.8	14.0	–0.070	0.307
18.0	17.8	16.5	14.8	14.0	–0.078	0.073

(Dash) Parameter was not measured.

Table 4. Some statistical parameters of the distributions of the measured specific CH_4 and CO_2 fluxes (mg C/(m^2 h)) and other integral parameters

Measurement point	Median of specific fluxes (number of measurements)		Variability (for the set of specific CO_2 fluxes)*	Mean temperature, °C				
					soil, depth, cm			
	CO_2	CH_4		air	0	5	10	15
T.Plo.For.1.25	76 (5)	–0.00 (6)	0.26	14.8	14.5	13.0	11.6	11.9
T.Plo.For.1.26	195 (2)	–0.03 (2)	0.10	23.5	21.7	15.5	14.5	12.9
Plo.For.Iksa.R								
18.07.2013	371 (20)	–0.02 (6)	0.19	22.3	20.6	15.6	15.2	15.0
19.08.2013	361 (30)	–0.04 (7)	0.15	18.4	18.2	16.6	14.9	14.0
Plo.For.Razr	745 (18)	–0.09 (6)	0.38	21.8	19.6	17.2	16.3	16.3
Plo.For.Razr2	410 (9)	–0.05 (3)	0.24	22.2	22.1	16.1	14.7	14.0
Plo.For.Razr2.1	470 (9)	–0.05 (3)	0.13	21.6	21.3	16.4	15.0	14.0
Birch.For	664 (36)	–0.12 (6)	0.26	15.2	15.7	15.3	14.5	14.0

* Calculated as the ratio of the difference between the third and first quartiles divided by 2 to the median of the set of specific CO_2 fluxes.

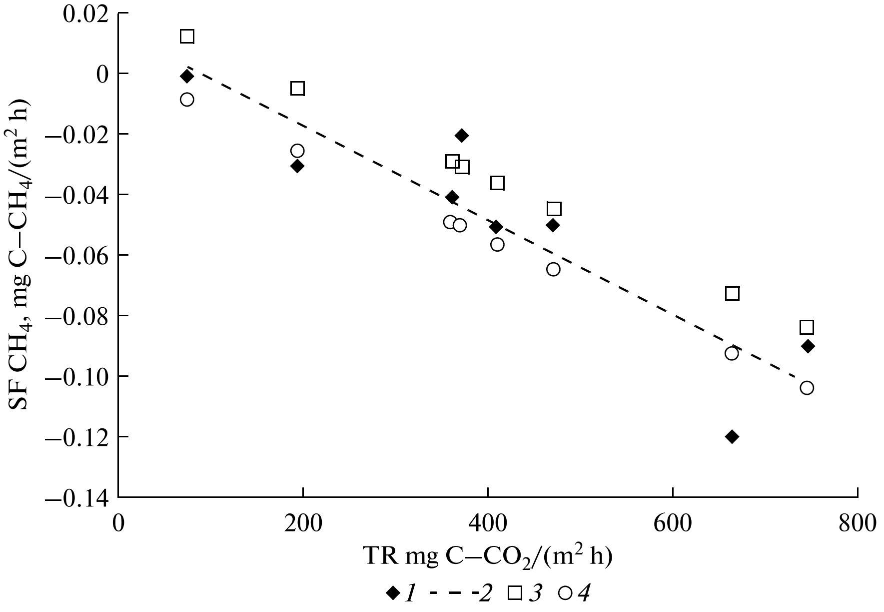
Table 5. Consumption of methane by soils in different forest ecosystems

Ecosystem	Measurement point coordinates	Specific methane fluxes, mg C–CH_4/(m^2 h)	Source
Mixed forest on gray forest soils, broad-leaved forest zone	54.81° N, 37.59° E	–0.05...–0.06 (May–October, mean monthly values)	[15]
Mixed forest on gray forest soils with different degrees of erosion, broad-leaved forest zone	54.82° N, 37.58° E	–0.004...–0.04 (June–September, individual values)	[14]
Birch forest on tundra soils, forest-tundra zone	54.72° N, 66.70° E	–0.01...–0.07 (June, mean monthly values)	[18]
Mixed pine–oak forest on gray forest soils, broad-leaved forest zone	43.94° N, 69.57° E	–0.11 (June, mean monthly value)	[18]
Pine forest on podzolic soils, taiga zone	42.50° N, 72.17° E	–0.10 (April–December, mean for 6 years)	[21]
Pine forest on podzolic soils, taiga zone	42.50° N, 72.17° E	–0.12 (April–December, mean for 6 years)	[21]
Beech–oak forest on mountain-meadow soils, broad-leaved forest zone	51.00° N, 9.85° E	–0.12 (April), –0.11 (June)	[36]
Beech forest on podzolic soils, broad-leaved forest zone	51.57° N, 10.17° E	–0.05 (April), –0.04 (June)	[36]

sphere. The neutrophilic mesophilic methanotrophs are associated with not only aquatic plants (hydrophythes), but also mesophilic terrestrial woody and herbaceous plants (in particular, the formation of stable associations of methanotrophs with some grasses and other plants was demonstrated in vitro) [5]. The consumption of methane by rhizospheric bacteria may be very significant [23, 33, 38].

The known relationship between the specific consumption (and not specific flux) of methane by plant roots (V, mg C–CH_4/g dry root biomass per hour), or, more precisely, by rhizospheric bacteria, and the concentration of methane in soil pores (C, mg C–CH_4/m^3) is described by the Michaelis–Menten equation:

$$V_r = V_{r,\max}C/(K_{r,m} + C), \qquad (2)$$



Relationship between the consumption of methane and the total respiration (TR) of the soil and the grass–moss layers: (*1*) medians of experimental data for each point; (*2*) linear regression on these data for specific fluxes (SFs) of $CH_4 = -(0.000157 \pm 0.000031)$ TR + (0.015 ± 0.014), $R^2 = 0.81$; (*3*) F_{ma} values calculated from the medians of the measured values of total soil respiration for each point; (*4*) sum of the F_{ma} values calculated from the medians of the measured values of total soil respiration for each point and the calculated F_s value.

where $V_{r,\max}$ is the maximum specific consumption rate by plant roots (mg C–CH$_4$/g dry root biomass per hour), and $K_{r,m}$ is the Michaelis constant equal to the methane concentration at which the methane consumption rate is half of the maximum value (mg C–CH$_4$/m^3). Under the assumption that the oxidation of methane in the soil mainly occurs in the upper 15-cm thick layer [17, 36, 37], the mean C value in this layer of analogous soils is 0.65 ± 0.07 mg C–CH$_4$/m^3 [36, 37]. Highly variable values of $V_{r,\max}$ and $K_{r,m}$ are reported by different authors; therefore, they should be averaged to avoid gross errors. The mean value of $K_{r,m}$ is 59.2 ± 12.6 mg C–CH$_4$/m^3 [27, 33], and the mean value of $V_{r,\max}$ is 0.023 ± 0.012 mg C–CH$_4$/g dry root biomass per hour.

The respiration rate of living plant biomass I_{lb}varies among the different species growing under temperate climatic conditions in the range from 0.5 to 2 mg C–CH$_4$/g dry root biomass per hour at 20°C[22]. From other sources, for umbraticolous sciophytes under forest canopy, this value varies from 0.4 to 1.1 mg C at the same temperature [41]. Therefore, we take $I_{lb} = 1 \pm 0.3$ mg C–CO$_2$/g dry root biomass per hour (our measurements were also performed at temperatures close to 20°C). Thus, the living aboveground biomass of the grass–moss layer B_l (g dry organic matter/m^2) can be estimated as follows:

$$B_l = (\mathrm{TR} - \mathrm{RSR})/I_{lb}, \tag{3}$$

where RSR is the respiration of soil and roots, mg C–CO$_2$/(m^2 h). The mean RSR value is about 160 ± 40 mg C–CO$_2$/(m^2 h) for mixed forests on podzolic soils in July–August [25, 39, 40]. The living aboveground/root biomass ratio for the grass–moss layer (p) varies in the range of 0.50–0.65 [26, 44]; hence, its mean value is 0.57 ± 0.07. Thus, the root biomass B_r (g dry organic matter/m^2) can be expressed as follows:

$$B_r = p(\mathrm{TR} - \mathrm{RSR})/I_{lb}. \tag{4}$$

Then, the simulated value of CH$_4$ consumption due to the root-associated methanotrophy (T_m, mg C–CH$_4$/(m^2 h)) can be expressed as follows:

$$F_{ma} = p(\mathrm{TR} - \mathrm{RSR})V_{r,\max}C/((K_{r,m} + C)\, I_{lb}). \tag{5}$$

The calculated F_{ma} values (average error was 0.025 mg C–CH$_4$/(m^2 h)) were found to be close to the measured values of specific CH$_4$ fluxes, and the slope of the linear relationship between the F_{ma} values and the total soil respiration was –0.000202, which well agreed with the slope of the relationship between the specific CH$_4$ fluxes and the total soil respiration calculated from experimental data using linear regression: –(0.000157 ± 0.000031).

The activity of free-living methanotrophs can be estimated from the data on the consumption of methane by the soil free from plants. In this case, the Michaelis–Menten equation will be as follows:

$$V_s = V_{s,\max}C/(K_{s,m} + C), \tag{6}$$

where $V_{s,\max}$ is the maximum rate of specific consumption by the soil (μg C–CH$_4$/kg dry soil per hour), and $K_{s,m}$ is the Michaelis semisaturation constant for soils (mg C–CH$_4$/m^3). According to literature data

[20, 35], $V_{s,\max} = 1.62 \pm 4.26$ and $K_{s,m}$ 8.64 ± 27.24 (median ± standard deviation for the soils analogous to those under study). Then, the consumption of methane by the free-living methanotrophs can be calculated from its consumption by the soil (F_s, mg C–CH_4/(m^2 h)) using the following equation:

$$F_s = dhV_s, \tag{7}$$

where d is the soil density, kg/m^3 (for the studied soils, the typical value is 1200), and h is the thickness of the soil layer in which an intensive oxidation of methane by free-living methanotrophs occurs, m. As was noted above, h can be taken equal to 0.15 ± 0.03 m. Then, F_s is 0.022 ± 0.080 mg C–CH_4/(m^2 h).

Thus, the theoretically calculated sum of plant-associated and free methanotrophies well agrees with the experimentally measured values, although it slightly exceeds them (figure). However, the performed calculations have some vulnerabilities. At the calculation of plant-related methanotrophy, the parameters $V_{r,\max}$ and $K_{r,m}$ for the Michaelis–Menten equation were found in the literature only for the bog and waterlogged ecosystems; therefore, their use for forest ecosystems bears some risks. The calculation of free methanotrophy involves the high variability of parameters $V_{s,\max}$ and $K_{s,m}$, which can also make the consumption prediction unreliable. Thus, the presented theoretical concept needs further support by data.

The effect of other factors like moisture, soil pH and temperature [21], and mineral nitrogen inhibiting the oxidation of methane [8] must also not be ignored; however, no statistically significant correlation between the soil temperature at any depth and the specific CH_4 fluxes was found in the current work.

CONCLUSIONS

(1) The median of specific CH_4 fluxes to the soil was –0.05 mg C/(m^2 h) for the entire set of measurements (the negative flux indicates the consumption of methane by the soil), which almost coincided with the values recorded in other forest ecosystems of the boreal zone.

(2) A statistically significant ($R^2 = 0.81$) linear relationship was revealed between the specific CH_4 fluxes to the soil and the total respiration of the grass–moss layer in forest ecosystems.

(3) The methane consumption by the soil with consideration for root-related methanotrophy was calculated from available literature data; from the obtained results, the experimental values of specific CH_4 fluxes were predicted, and the relationship between the consumption of methane by the soil and the total respiration of the grass–moss layer was determined. The consideration of free methanotrophy not related to plants resulted in an even better agreement with the experimental data, which confirmed the importance of both sinks for atmospheric methane.

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