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Methane uptake rates in Japanese forest soils depend on the oxidation ability of topsoil, with a new estimate for global methane uptake in temperate forest

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Abstract To clarify the reason for the higher CH_4 uptake rate in Japanese forest soils, twenty-seven sites were established for CH_4 flux measurement. The first order rate constant for CH_4 uptake was also determined using soil core incubation at 14 sites. The CH_4 uptake rate had a seasonal fluctuation, high in summer and low in winter, and the rate correlated with soil temperature at 17 sites. The annual CH_4 uptake rates ranged from 2.7 to 24.8 kg CH_4 ha^{-1} y^{-1} (the average of these rates was 9.7 or 10.9 kg CH_4 ha^{-1} y^{-1}, depending on method of calculation), which is somewhat higher than the uptake rates reported in previous literature. The averaged CH_4 uptake rate correlated closely with the CH_4 oxidation rate of the topsoil (0–5 cm) in the study sites. The CH_4 oxidation constant of the topsoil was explained by a multiple regression model using total pore volume of the soil, nitrate content, and C/N ratio ($p < 0.05$, $R^2 = 0.684$). This result and comparison with literature data suggest that the high CH_4 uptake rate in Japanese forest soils depends on the high porosity probably due to volcanic ash parent materials. According to our review of the literature, the CH_4 uptake rate in temperate forests in Europe is significantly different from that in Asia and North America. A new global CH_4 uptake rate in temperate forests was estimated to be 5.4 Tg y^{-1} (1 SE is 1.1 Tg y^{-1}) on a continental basis.

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Introduction

Methane (CH_4) is an important greenhouse gas and the terrestrial oxidation of CH_4 accounts for 2–10% of the global CH_4 sink (Prather et al. 1996). The uptake of CH_4 by soils has been observed in many forest soils around the world (Keller et al. 1986; Castro et al. 1995; Singh et al. 1997; Priemé and Christensen 1999; Smith et al. 2000; Ishizuka et al. 2000, 2005; Kiese et al. 2003; Price et al. 2004; Nakano et al. 2006; Morishita et al. 2007). Although the CH_4 uptake shows high variation among forests (Smith et al. 2000; Ishizuka et al. 2000; Price et al. 2004; Dutaur and Verchot 2007), global empirical models of CH_4 uptake rate have been developed based on a limited number of flux observations (Dörr et al. 1993; Potter et al. 1996; Smith et al. 2000; Dutaur and Verchot 2007) and a mechanistic approach using controlling factors and global-scale database related to the factors (Ridgwell et al. 1999; Curry 2007; Dutaur and Verchot 2007). Because these models have been developed based on the flux measurements in various ecosystems, the estimate could be biased by the spatial distribution of measurements, for example, a high concentration in eastern North America, Western Europe and northern South America (Dutaur and Verchot 2007).

In estimating CH_4 flux, many studies have considered its seasonal fluctuation of the flux in a forest. Regarding fluctuation of CH_4 uptake rate in an individual ecosystem, soil moisture variation has been considered to be a crucial factor (Steudler et al. 1989; Born et al. 1990; Striegl 1993; Adamsen and King 1993; Koschorreck and Conrad 1993; Castro et al. 1995; Czepiel et al. 1995; Price et al. 2004). A few researchers have suggested temperature is important for explaining the seasonal fluctuation of CH_4 oxidation in an ecosystem (Castro et al. 1995; Priemé and Christensen 1997). However, because few studies have dealt with the variation of CH_4 flux on a regional scale (Dörr et al. 1993), the predominant factor affecting the variation of the CH_4 uptake rate among the independent forests is not clear. A comparison of the CH_4 uptake rates among different forests would be valuable for understanding the variation among the forests. These analyses may provide useful information for improving the current estimation of global CH_4 uptake (Dörr et al. 1993; Potter et al. 1996; Dutaur and Verchot 2007).

Recently, high CH_4 uptake rates exceeding 5 mg CH_4 m^{-2} d^{-1} have been reported in some forests (Singh et al. 1997; Ishizuka et al. 2000; Tamai et al. 2003; Morishita et al. 2007). In Japan, CH_4 flux measurements have been carried out at more than 50 sites in this decade (Ishizuka et al. 2000; Tamai et al. 2003; Morishita et al. 2007; Ishizuka et al. this study). Except for very high rates in savanna and tropical forests (Singh et al. 1997), Japanese forests showed high CH_4 uptake rates that were at the upper end among temperate forest soils in the world (Dutaur and Verchot 2007). However, the factors controlling these high CH_4 uptake rates in Japanese forests and associated background have not been well examined.

Our objectives are to confirm the high CH_4 uptake rate in Japanese forest soils and to clarify the factors affecting the variation among the sites in such high CH_4 consuming soils. Secondly, in the process of comparing CH_4 uptake rates between temperate forests in Japan and other countries, we noticed that the average CH_4 uptake rate in temperate forests in Europe could be different from those in Asia and North America. Therefore, we have proposed a new CH_4 uptake rate in temperate forests on a continental basis.

Materials and methods

Site description

We established twenty-seven sites in nineteen forest areas in Japan for CH_4 flux measurement. The sites ranged in latitude from 26°N to 44°N, which covers most of the Japanese Archipelago (Table 1). These forests are mainly humid temperate forests, with four exceptions: one subtropical forest (OK) and three sub-alpine coniferous forests (SK, OD1 and OD2). The mean annual soil temperatures at 5 cm depth of these forests range from 4 to 22°C. The mean annual rainfall for the last 10 years at the meteorological station nearest each site (Japan Meteorological Agency, Automated Meteorological Data Acquisition System: http://www.data.kishou.go.jp/) ranged from

Table 1 General information on the sites

Site	Lat.	Long	Elev. (m)	Vegetation[a]	Management type	Soil type[c]	MAP[d] (mm)	MAT[e] (°C)	Avg. soil temp. (°C)	Flux observation period	Number of samplings
SK	43°40′	143°06′	1,000	PJ, AS	Natural	Podzol	1,418	1.5	4.1[f]	Sep 99–Oct 01	8
JK	42°59′	141°10′	322	AS	Planted	Cambisol	1,268	5.5	7.3[f]	Jun 99–May 01	6
MM	42°55′	141°16′	440	AS	Planted	Cambisol	1,268	5.7	6.4[g]	Jun 99–Sep 99	4
HG1	42°59′	141°24′	240	BP, QM	Natural	Andosol	1,167	6.6	7.6[g]	Jun 98–Sep 99	12
HG2	42°59′	141°24′	260	BP, QM	Natural	Andosol	1,167	6.6	7.5 [g]	Jun 98–Sep 99	11
HG3	42°59′	141°23′	175	BP, QM	Natural	Andosol	1,167	7.2	8.3[f]	Jun 98–Aug 00	6
AP	40°00′	140°56′	825	FC	Natural	Andosol	1,207	6.1	6.9[f]	Jun 00–Nov 01	13
ANM	39°59′	140°24′	200	CJ	Planted	Cambisol	2,006	9.4	9.4 [g]	Jun 01–Nov 02	14
TZ	39°46′	140°43′	350	CJ	Planted	Andosol	2,188	7.5	9.6[f]	Jul 00–May 02	13
OG1	36°56′	140°35′	650	FC, FJ	Natural	Andosol	1,948	8.6	10.6[f]	May 95–Mar 02	30
OG2	36°56′	140°35′	650	FC, FJ	Natural	Cambisol	1,948	8.6	10.6[f]	Jul 95–Mar 98	13
OG3	36°56′	140°35′	650	CJ	Planted	Andosol	1,948	8.4	9.5[f]	Jun 97–Mar 02	18
OG4	36°56′	140°35′	650	QS, CA	Deforested	Cambisol	1,948	8.4	9.1[f]	Nov 96–Dec 97	6
HT1	36°35′	140°35′	380	CA	Mixed[b]	Cambisol	1,371	11.4	12.1[g]	Jul 97–May 98	6
HT2	36°35′	140°35′	380	CO, CJ	Planted	Cambisol	1,371	11.4	12.1[g]	Jun 97–Sep 97	4
KB1	36°18′	140°09′	470	CA, QM	Mixed[b]	Cambisol	1,310	11.5	11.1[g]	Aug 97–Jun 02	23
KB2	36°19′	140°09′	250	CO	Planted	Cambisol	1,310	12.7	12.0[f]	Apr 99–Jun 02	19
TK	36°10′	140°10′	330	CJ	Planted	Andosol	1,310	12.6	12.2[g]	May 95–Nov 95	6
KZ	36°01′	140°08′	22	CO	Planted	Andosol	1,203	13.6	14.0[g]	Feb 95–Aug 95	5
OT	35°55′	137°19′	1,350	CO	Planted	Andosol	3,502	10.1	6.4[g]	Aug 00–Dec 01	13
OD1	35°51′	138°39′	2,090	AV	Natural	Podzol	1,365	3.1	4.2[f]	Jun 99–Sep 01	14
OD2	35°51′	138°39′	2,080	LK	Planted	Podzol	1,365	3.1	5.2[f]	Jun 99–Sep 01	14
ST	35°14′	137°08′	630	CO	Planted	Cambisol	1,528	13.9	11.2[f]	Jul 00–Dec 01	14
IB	35°12′	137°34′	1,010	CO	Planted	Cambisol	1,972	8.6	9.3[f]	Jul 00–Dec 01	14
HS	34°24′	132°43′	240	PD	Natural	Cambisol	1,513	13.1	15.1[g]	Oct 01–Dec 01	3
KH	33°08′	130°43′	165	CO, CJ	Planted	Cambisol	2,072	14.0	14.2[f]	May 00–Mar 03	35
OK	26°31′	127°59′	100	CC	Natural	Alisol	2,131	21.7	21.5[f]	Apr 99–Jan 02	7

[a] AV *Abies veitchii*, AS *A. sachalinensis*, BP *Betula platyphylla*, CA *Carpinus* spp., CC *Castanopsis cuspidata*, CJ *Cryptomeria japonica*, CO *Chamaecyparis obtusa*, FC *Fagus crenata*, FJ *F. japonica*, LK *Larix kaempferi,* PD *Pinus densiflora*, PJ *Picea jezoensis*, QM *Quercus mongolica*, QS *Q. serrata*

[b] Unsuccessful afforestation (overgrown by natural vegetation)

[c] WRB classification (ISSS Working Group RB 1998)

[d] Mean annual rainfall between 1993–2002 at the nearest meteorological station of the Japan Meteorological Agency

[e] Mean annual temperature between 1971–2000 (Japan Meteorological Agency)

[f] Average soil temperature through a year measured with a thermorecorder at 1-h intervals

[g] Estimate based on the mean annual air temperature at the nearest meteorological station and the elevation of the site

1,200 to 3,500 mm (1,630 mm on average). The northern sites (SK, HG, JK, MM, AP, ANM and TZ) and the high-altitude sites (OD and OT) are usually covered with snow from December through April. The mid-latitude sites (OG, HT, KB, TK, KZ, ST and IB) are sometimes covered with snow for a few weeks in winter.

The ages of trees in all plantations were older than 20 years. Four soil types [Cambisol, Andosol, Podzol, and Alisol (International Society of Soil Science (ISSS) Working Group RB 1998)] exist at the study sites, and most sites are affected by volcanic ash deposition to some extent. The general soil properties are shown in Table 2. Further information, such as

soil texture and microbial biomass C in each site, can be found elsewhere (Ishizuka et al. 2006).

Flux measurement

We measured the CH_4 fluxes using a static chamber method (Sakata et al. 2004). Three to five replicate stainless steel tubes (15-cm length, 40-cm diameter) at each site were inserted in the soil to 5 cm in depth. The chambers were fixed to their respective locations throughout the experimental period. At 0, 10 and 20 min elapsed time, a gas sample was taken from the chamber with a syringe and put into a glass vial topped with a butyl rubber stopper which had been evacuated beforehand in the laboratory. The gas concentrations were determined with a gas chromatograph equipped with a flame ionization detector (GC-14B, Shimadzu Co., Kyoto, Japan). A 5-mL gas sample was used for analysis. Standard calibration was made using standard gases of 1.25 and 2.00 μL CH_4 L^{-1} (Sumitomo Seika Chemicals Co., Osaka, Japan).

We calculated fluxes using a non-linear model (Hutchinson and Mosier 1981), in which the chamber volumes were corrected according to the air pressure corresponding to the altitude of the plot. We basically measured the CH_4 fluxes monthly but avoided taking samples on heavy-rain days. When snow covered the surface of the chamber, we did not take a gas sample. The air temperature 1 m above the ground and the soil temperature at 5 cm depth were also measured using a portable thermometer (SK-1250MC, Sato Co., Tokyo, Japan). At 14 sites where the core incubation analysis mentioned below was conducted, we measured soil temperatures at depths of 5 and 15 cm, at hourly intervals using a thermo recorder (TR-72S, T and D Co., Tokyo, Japan).

At 17 sites in which the CH_4 uptake rate significantly correlated with the soil temperature at 5 cm depth, we estimated annual CH_4 uptake by the summation of hourly CH_4 uptake for a year calculated by hourly data of soil temperature. At the other eight sites (SK, JK, HG3, ANM, TZ, OG4, HT2, OD1) at which the CH_4 uptake rate did not significantly correlate with the soil temperature at 5 cm depth and the CH_4 uptake rate was relatively stable among the seasons (data not shown), we calculated the annual CH_4 uptake by extrapolating the average CH_4 flux to the unobserved period. We did not estimate annual CH_4 uptake for two sites (HS and OK) due to both the low number of samplings and the unclear trend of CH_4 flux fluctuation. We assumed that snow cover hinders the diffusion of CH_4 in air to topsoil, thus the CH_4 uptake in the snowy season was smaller than the estimate mentioned above. Therefore, we tested two methods to calculate the annual amount of CH_4 uptake: one was the method mentioned above (hereafter, original method, on the assumption that snow did not affect CH_4 uptake rate) and the other is a method which excludes the CH_4 uptake in the snow cover season in the snowy sites (hereafter Method 2, on the assumption that there was no uptake in the snow season). The original method provides the maximum CH_4 uptake and Method 2 provides minimum CH_4 uptake at snowy sites.

Soil sampling and analysis

Soil for chemical analysis was sampled from depths of either 0–5, 10–15 and 20–25 cm, or 0–5, 5–10, and 10–15 cm. All soils were sieved with a 2-mm-mesh sieve and stored in a refrigerator at 4°C until analysis. Inorganic ammonium and nitrate were determined by a flow-injection analyzer (Aquatec 5400 analyzer, Tecator, Sweden) with an extractant of 10 g fresh soil shaken with 100 ml 2 M KCl for 1 h. Soil water content was calculated by the weight difference between before and after oven drying at 105°C for 24 h. A portion of the soil sample was air-dried and finely ground and sieved through 0.5-mm mesh. The soil total carbon and nitrogen contents were measured for these soils using an NC analyzer (NC-800, Sumitomo Chemical Co., Osaka, Japan).

Soil core analysis

Cylindrical soil samples were collected using a 100-mL (5 cm in diameter and 5.1 cm in height) stainless tube from the same sampling depths for chemical analysis at each plot. Triplicate samples were collected from each depth. Three-phase distribution was measured with a gas pycnometer (DIK-1121, Daiki Rika Kogyo Co., Tokyo, Japan).

We evaluated a first order rate constant for CH_4 uptake of soil at 14 sites (TZ, OG1, OG2, OG3, HT1, HT2, KB1, KB2, TK, OD1, OD2, ST, IB, HS), by soil core incubation (Ishizuka et al. 2000). An intact soil core was placed in a 500-mL incubation jar

Table 2 Soil characteristics of 0–5 cm of soil

	pH (H_2O)	Water content (kg kg^{-1})	Total C (mg g^{-1})	Total N (mg g^{-1})	Bulk density (Mg m^{-3})	Inorganic N		Pore volume (m^3 m^{-3})	Ave. gas-filled porosity (m^3 m^{-3})
						NH_4–N (μg g^{-1})	NO_3–N (μg g^{-1})		
SK	4.2	0.78	86	4.6	ND[a]	17.2	2.0	ND[a]	ND[a]
JK	5.1	0.45	50	3.1	ND[a]	ND[a]	ND[a]	ND[a]	ND[a]
MM	5.3	0.59	55	4.0	0.46	25.0	2.3	0.81	0.54
HG1,2	6.0	0.68	78	5.7	0.55	19.7	1.7	0.77	0.40
HG3	6.2	1.08	104	5.6	0.36	11.8	0.5	0.75	0.36
AP	4.5	1.17	129	8.7	0.41	21.5	7.8	0.82	0.35
ANM	5.2	ND[a]	300	12.5	ND[a]	ND[a]	ND[a]	ND[a]	ND[a]
TZ	5.8	1.23	140	8.6	0.33	21.7	12.9	0.87	0.47
OG1	4.9	1.67	230	13.0	0.33	13.8	15.3	0.86	0.30
OG2	4.8	0.78	54	4.0	0.51	9.0	1.2	0.80	0.40
OG3	4.5	1.04	162	10.4	0.35	ND[a]	ND[a]	0.90	0.53
OG4	4.8	0.64	94	5.6	0.58	10.6	6.4	0.80	0.42
HT1	4.5	0.50	48	3.1	0.55	13.5	18.5	0.80	0.52
HT2	4.2	0.99	88	4.5	0.48	10.0	3.4	0.77	0.30
KB1	4.6	0.94	125	10.2	0.34	10.0	9.2	0.87	0.55
KB2	ND[a]	1.32	148	9.1	0.30	ND[a]	ND[a]	0.89	0.50
TK	4.4	1.45	169	11.0	0.31	14.9	48.8	0.87	0.41
KZ	ND[a]	ND[a]	ND[a]	ND[a]	ND[a]	ND[a]	ND[a]	ND[a]	ND[a]
OT	4.1	1.68	133	9.2	0.31	20.6	22.3	0.87	0.35
OD1	3.7	1.18	212	11.6	0.32	14.9	14.2	0.89	0.52
OD2	4.0	0.62	132	7.5	0.55	13.6	9.3	0.80	0.46
ST	4.2	0.45	24	1.7	0.79	9.7	1.9	0.69	0.34
IB	4.8	1.04	80	4.6	0.51	20.4	5.3	0.83	0.30
HS	4.3	0.36	71	3.4	0.88	13.1	0.3	0.67	0.36
KH	4.5	0.61	42	2.7	0.84	13.8	0.1	0.68	0.17
OK	4.9	0.25	50	2.4	0.80	8.8	0.4	0.66	0.46

[a] Not determined

stopped with a butyl rubber stopper, and the headspace was replaced with 10 μL L^{-1} standard gas (air balance). The gas in the headspace was sampled at appropriate time intervals using a 1-mL gas-tight syringe, until the concentration either became lower than 0.2 μL L^{-1} or 24 h had passed. The CH_4 concentration Ct (μL L^{-1}) at a time t (h) is expressed as

$$\mathrm{Ct} = C_0 \times e^{-kt} \quad (1)$$

where C_0 (μL L^{-1}) is the CH_4 concentration of the headspace at the beginning, and k (h^{-1}) is the reaction rate constant. The k value obtained by this core incubation method is considered to give a first order rate constant for CH_4 consumption at CH_4 concentrations around ambient air.

Statistical analysis

We used multiple regression analysis to estimate the k value in 0–5 cm deep soil using soil chemical, physical parameters adjusted to 100 mL soil quantity. Soil pH, water content, total carbon, total nitrogen, CN ratio, NH_4 and NO_3 content, and total pore volume were supplied for the regression analysis. We used the forward selection method to select the valuable parameters for the regression analysis ($p < 0.20$).

Results

Seasonal fluctuation of CH_4 flux at each site

All CH_4 fluxes measured showed negative values (i.e., CH_4 was oxidized by soils) except for one observation at OK. The CH_4 uptake rate had a seasonal fluctuation such as high in summer and low in winter, as seen in the example of KH in Fig. 1. The soil water content did not have apparent seasonal fluctuation, although it was high in winter and low in summer at some sites. In 17 plots, CH_4 uptake rate in each ecosystem significantly correlated with the soil temperature at 5 cm depth ($p < 0.05$, the average correlation coefficient was 0.726, Table 3). No correlations were found between soil water content and CH_4 flux for any site fluctuation ($p > 0.05$).

The average CH_4 uptake rates ranged from 0.19 to 6.87 mg CH_4 m^{-2} d^{-1} (Table 3). The amounts of annual CH_4 uptake ranged from 2.7 to 24.8 kg CH_4 ha^{-1} and averaged 10.9 kg CH_4 ha^{-1} at 25 sites. By adopting Method 2 for the snow-covered area, the average amount of CH_4 uptake was reduced to 9.7 kg CH_4 ha^{-1}. The Q_{10} value of the CH_4 uptake rate between 5 and 15°C ranged from 1.14 to 2.57 (average and standard deviation were 1.51 and 0.35, respectively, $n = 17$).

Intact soil core incubation analysis

The k value in the Eq. 1 ranged widely from 0.039 to 1.35 h^{-1}. The depth with the maximum k value in a profile differed by site (Fig. 2). At seven of 14 sites, k values for soil deeper than 5 cm were greater than those at 0–5 cm depth.

Variation in CH_4 flux among the sites and its relationship with soil properties

The CH_4 uptake rate in all chamber correlated with the soil gas-filled porosity at 0–5 cm depth (Fig. 3, $R^2 = 0.206$, $p < 0.001$, $n = 217$). The CN ratio at 0–5 cm depth negatively correlated with averaged CH_4 uptake rate at our study sites ($R^2 = 0.441$, $p < 0.01$). Other parameters in 0–5 cm depth soil did not show significant correlation with averaged CH_4 uptake rate (pH, $R^2 = 0.009$; water content, $R^2 = 0.014$; total C, $R^2 = 0.009$; total N, $R^2 = 0.043$; bulk density, $R^2 = 0.095$; inorganic ammonium content, $R^2 = 0.005$; inorganic nitrate content, $R^2 = 0.000$). The averaged CH_4 uptake rate closely correlated with the k value of 0–5 cm depth soil at the study sites (Fig. 4). As a result of multiple regression analysis, the k value was explained by NO_3 content (mg N) and soil pore volume (PV)(mL) in 100 mL soil, and CN ratio as follows ($R^2 = 0.684$):

$$k \text{ value} = -0.712\ NO_3 + 0.046\ PV - 0.060\ CN \text{ ratio} - 1.866$$

Discussion

Factors affecting fluctuation of the methane uptake rate in each forest

The seasonal fluctuations of CH_4 uptake rate correlated with soil temperature at 60% of the sites. The range of Q_{10} value of the CH_4 uptake rate (1.14–2.57) was comparable with the range in previous reports [e.g., 1.3 (Priemé and Christensen 1997), 1.2–2.0 (Crill 1991) and 1.5 (Born et al. 1990)]. The average Q_{10} value (1.51) was about a half of the Q_{10} value of

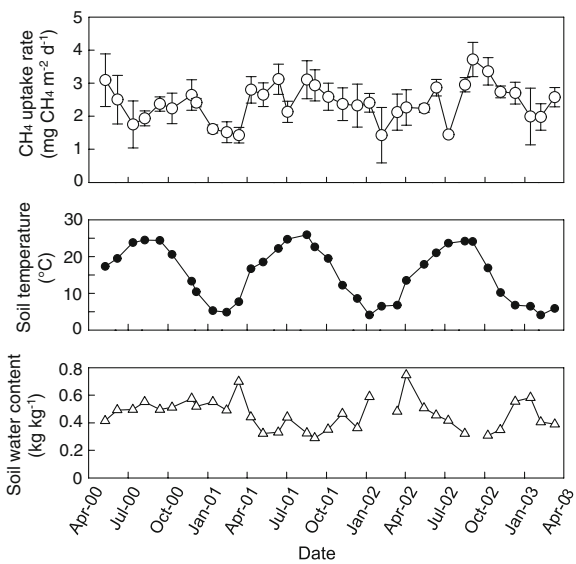

Fig. 1 Fluctuation of CH_4 uptake rate (*upper, open circles* with 1 SD *error bars*), soil temperature at 5 cm depth (*middle, closed circles*), and soil water content (*lower, open triangle*) at KH

Table 3 Result of flux measurement and annual uptake rate and its parameters

Site	Min.	Max.	Average	Regression parameter[a]		Q_{10} (5–15°C)	Annual uptake kg CH_4 ha^{-1}	
	mg CH_4 m^{-2} d^{-1}			R^2	P		Original method	Method 2
SK	2.56	3.97	2.93	0.012	0.60	ND[d]	10.71[b]	7.16
JK	1.44	1.90	1.73	0.242	0.32	ND[d]	6.30[b]	4.21
MM	4.16	5.71	4.92	0.922	0.04	1.45	14.48[c]	11.09
HG1	2.66	5.75	4.13	0.776	0.00	1.64	11.42[c]	9.55
HG2	2.13	4.22	3.31	0.536	0.01	1.52	9.33[c]	7.57
HG3	2.20	3.27	2.58	0.581	0.08	ND[d]	9.41[b]	6.29
AP	1.48	3.35	2.32	0.377	0.03	1.38	7.38[c]	5.53
ANM	0.75	1.41	1.09	0.581	0.08	ND[d]	3.99[b]	2.67
TZ	1.54	3.75	2.40	0.248	0.08	ND[d]	8.76[b]	5.86
OG1	0.05	4.88	2.45	0.459	0.00	1.71	8.84[c]	NE[e]
OG2	3.60	5.85	4.72	0.462	0.01	1.22	16.51[c]	NE[e]
OG3	1.04	5.40	3.97	0.366	0.01	1.33	15.20[c]	NE[e]
OG4	3.83	5.59	4.53	0.447	0.15	ND[d]	16.52[b]	NE[e]
HT1	2.02	4.23	3.19	0.859	0.01	1.51	10.85[c]	NE[e]
HT2	1.52	1.81	1.65	0.105	0.68	ND[d]	6.03[b]	NE[e]
KB1	3.02	10.48	6.87	0.591	0.00	1.39	24.78[c]	NE[e]
KB2	2.91	9.40	4.71	0.522	0.00	1.44	16.42[c]	NE[e]
TK	0.78	2.99	1.78	0.744	0.03	2.57	3.79[c]	NE[e]
KZ	2.39	4.62	3.55	0.797	0.04	1.52	11.93[c]	NE[e]
OT	2.04	4.20	2.71	0.386	0.02	1.27	9.10[c]	6.66
OD1	2.14	4.24	2.91	0.078	0.33	ND[d]	10.61[b]	7.09
OD2	1.75	4.27	3.19	0.492	0.01	2.02	8.02[c]	6.67
ST	1.35	2.72	1.95	0.428	0.01	1.26	6.78[c]	NE[e]
IB	3.18	7.07	4.48	0.301	0.04	1.25	15.44[c]	NE[e]
HS	0.47	1.08	0.77	0.753	0.33	ND[d]	ND[d]	NE[e]
KH	1.20	3.71	2.36	0.237	0.03	1.14	8.72[c]	NE[e]
OK	-0.01	0.55	0.19	0.006	0.87	ND[d]	ND[d]	NE[e]

[a] Regression parameter of the equation: (flux) = A + $B^{(\text{soil temperature})}$

[b] Estimation using average CH_4 uptake rate

[c] Estimation using soil temperature data

[d] Not determined due to low temperature-dependency

[e] Not estimated because of no snow cover effect

CO_2 flux (2.97 on average) (Ishizuka et al. 2006). In the ambient air, the CH_4 concentration was too low to become saturated in CH_4 consumption rate and the CH_4 uptake rate was limited by the rate of CH_4 diffusion in the soil rather than enzymatic activity (King and Adamsen 1992). Therefore, the temperature-dependency in CH_4 uptake rate was low due to the low temperature-dependency of the CH_4 diffusion rate in the soil (King and Adamsen 1992; Smith et al. 2003). On the other hand, the Q_{10} value of CO_2 flux was mainly regulated by enzymatic activity under the oxic condition in this study and the value was consistent with the response of enzyme systems (King and Adamsen 1992).

The water content did not play an important role in seasonal fluctuation in our observation. Because Japanese forests are usually located on slopes in mountainous areas and their soils generally have high porosity, the soils have good drainage properties and maintain high aeration in the topsoil. Therefore,

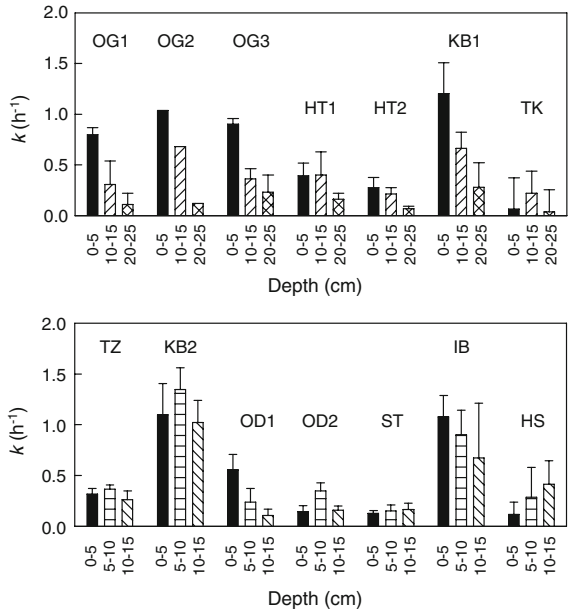

Fig. 2 Vertical distribution of methane uptake rate constant (k) at each site. The *vertical error bar* means 1 SD of the triplicate measurement (the result at OG2 was the average of two replicates)

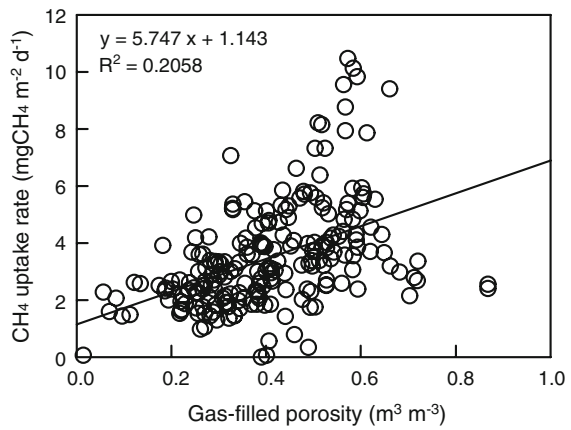

Fig. 3 Relationship between soil gas-filled porosity at 0–5 cm depth and CH_4 uptake rate at all sites ($n = 217$)

despite frequent rainfall in Japan, the soils tend to maintain near-natural water holding conditions in the topsoil for a long time. In the present study, there was less variation in the soil water content when sampling at once-a-month intervals. This lower variation in soil water content is likely to be one reason for the low sensitivity of the CH_4 uptake rate to the water content in the seasonal fluctuation.

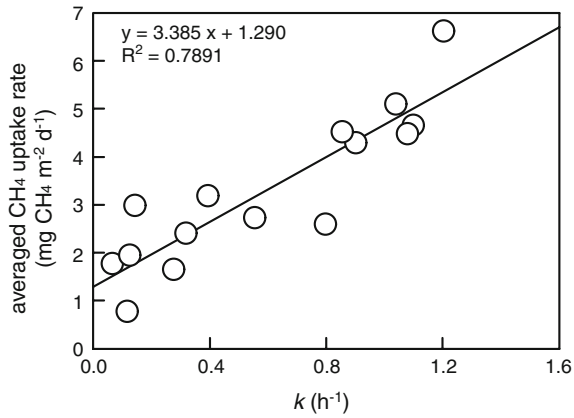

Fig. 4 Relationship between k-value of 0–5 cm depth and averaged CH_4 uptake rate at 15 sites

Another possible reason is that we avoided sampling on heavy-rain days, so we probably did not take enough measurements during times of high water content. This indicates that the CH_4 uptake rate in our study may have been overestimated because low CH_4 uptake rate during heavy rain was not taken into account. However, in an oak forest in the UK, the annual flux estimated using soil water potential was only 6% greater than the average of monthly flux (Bradford et al. 2001). Furthermore monthly sampling adequately estimated rates of CH_4 flux in a mixed deciduous forest in North America (Bowden et al. 2000). These results, together with the high drainage properties of Japanese forest soils, suggest that our estimates of annual CH_4 uptake rate without the measurement on heavy-rain days may possibly have been overestimated but was not seriously biased.

Factors affecting the differences in CH_4 uptake rates among the sites

With regard to the difference in the CH_4 uptake rate among the sites, the averaged CH_4 uptake rate correlated closely with the k value of the topsoil at the study sites (Fig. 4), which suggests that the CH_4 oxidation ability of the topsoil plays the most important role in the variation of the annual amount of CH_4 uptake in Japanese forest soils. According to the multiple regression analysis, the k value of the soil at 0–5 cm depth positively depended on total pore volume of the soil and negatively depended on

NO_3 content and C/N ratio. This result is comparable with the regulation by soil porosity (Striegl 1993) and inhibition by inorganic nitrogen for CH_4 oxidation (Steudler et al. 1989; Adamsen and King 1993; Sitaula et al. 1995). It also suggests that soil physical, chemical, and biological factors together all affect the CH_4 uptake rate in surface soils in Japan. However, it is possible that other factors that inhibit CH_4 oxidation contribute to the variation in the CH_4 uptake rate in forest soils, such as aluminum (Tamai et al. 2003), monoterpenes (Amaral and Knowles 1998), and possibly ammonium, which was not selected as an explanatory factor for CH_4 oxidation in this study, but is a well-known CH_4 oxidation inhibitor (King and Schnell 1994).

Comparison of CH_4 uptake rate with other reports

The average annual CH_4 uptake rate in this study, from 9.7 to 10.9 kg CH_4 ha^{-1} y^{-1}, was comparable with the value for Japanese forests (Ishizuka et al. 2000; Tamai et al. 2003; Morishita et al. 2007) and was much higher than the average value of 1.6 kg CH_4 ha^{-1} y^{-1} in northern European soils (Smith et al. 2000). The frequency distribution of annual methane uptake rates in forests in Table 4, relevant to annual estimation, was modified ($n = 238$) from Smith et al. (2000).

The median range of annual CH_4 uptake rate in Asia, Europe and North America (kg CH_4 ha^{-1} y^{-1}) were from 6.4 to 12.8, from 1.6 to 3.2, from 3.2 to 6.4, respectively (Table 4). The average and standard error of annual CH_4 uptake rate in Asia, Europe and North America in Table 4 (kg CH_4 ha^{-1} y^{-1}) were 7.8 ± 0.6, 3.9 ± 0.5, 7.4 ± 1.2, respectively.

In spite of the low accuracy for accounting for annual uptake rates due to the limited number of samplings, more than 32 forests were available for statistical analysis for averaged CH_4 flux in temperate forests (Castro et al. 1994b; MacDonald et al. 1996; Priemé et al. 1996, 1997 in addition to the list of papers in Table 4). The average of CH_4 uptake rate observed in temperate forests in Asia and North America is significantly greater than that of temperate forests in Europe, and is also greater than that of tropical and boreal forests (Scheffe-test, Fig. 5). Although the global CH_4 uptake rate in temperate forests has been estimated in several reports, the area of temperate forests has unexpectedly differed among the reports. Potter et al. (1996) estimated the CH_4 uptake rate was 5.7 Tg y^{-1} in temperate forests corresponding to 13.3×10^6 km^2 of temperate forests (the sum of cool and warm temperate forests in Table 3 in Potter et al. 1996). Curry (2007) estimated the CH_4 uptake rate was 11.3 Tg y^{-1} in temperate forests corresponding to 42.8×10^6 km^2 of temperate forests (the sum of cool, warm and subtropical forests in Table 1 in Curry 2007). Dutaur and Verchot (2007) estimated the CH_4 uptake rate was 3.0 Tg y^{-1} (1 SE is 1.1 Tg y^{-1}) in temperate forests corresponding to 5.82×10^6 km^2 of temperate forests.

We combined the FAO (2001) figures for the area of subtropical and temperate forests in Asia (Table 20-1 and -2), Europe (Table 27-1 and -2), North and Central America (Table 33-1 and -2), and Oceania (Table 38-1 and -2) to derive our figures for temperate forests. According to these calculations (Table 5), total temperate forest area was 8.43×10^6 km^2, between the figures cited by Dutaur and Verchot (2007) and Curry (2007). When we extrapolate the average CH_4 uptake rate to these regions, the CH_4 uptake rate in temperate forest soils is estimated to be 5.4 Tg y^{-1} (1 SE is 1.1 Tg y^{-1}, Table 5), which has a somewhat lower standard error than the estimate by Dutaur and Verchot (2007). This estimate is somewhat higher than that of Dutaur and Verchot (2007), and comparable with that of Potter et al. (1996) even though their value for area of temperate forests was 70% larger than ours.

The predominant factor to make the variation in CH_4 uptake rate among the forests might differ by the scale. For example, the bulk density might be an effective parameter for estimating CH_4 uptake rate on a global scale, but it was less valuable for making estimations for the variation in European forests (Fig. 6).

The multiple regression analysis and Fig. 6 indicated that high porosity due to low bulk density is responsible for high CH_4 uptake rate in Japanese forest soils. Chemical and biological factors such as CN ratio and nitrate content might be valuable only for explaining the variation of CH_4 uptake rate in Japanese forest soils. However, it is possible that the global estimates can be improved by reflecting the effects of inhibitors such as nitrate content in the soil, although this hypothesis needs to be tested by examining forests in other counties.

The critical lack of data for Asia, Africa and Oceania is still priority for IGBP/IPCC (Smith et al.

Table 4 Methane oxidation rates in forest reported for different climatic zones (modification from Smith et al. 2000)

	Methane oxidation rate (kg CH_4 ha^{-1} y^{-1})									
	<0.1	0.1–0.2	0.2–0.4	0.4–0.8	0.8–1.6	1.6–3.2	3.2–6.4	6.4–12.8	12.8–25.6	25.6–51.2
Temperate forest/woodland										
Asia	0	0	1	0	3	6	18	30	12	0
Europe	0	2	3	4	12	13	10	12	2	0
North America	0	0	0	1	2	6	7	2	8	0
Oceania	0	0	0	0	0	0	1	1	0	0
Tropical/subtropical forest	1	0	2	0	4	8	17	3	0	4
Boreal forest	3	0	5	11	16	5	2	1	0	0

The sources of data are listed below

Temperate forest/woodland in Asia: Morishita et al. 2007, 2004, Jang et al. 2006, Du et al. 2004, Dong et al. 2003, Kagotani et al. 1999, Morishita and Hatano 1999, Ishizuka et al. (this study)

Temperate forest/woodland in Europe: Fiedler et al. 2005, Castaldi and Fierro 2005, Merino et al. 2004, Borken et al. 2002, 2003, Butterbach-Bahl and Papen 2002, Butterbach-Bahl et al. 2002, Bradford et al. 2001, Steinkamp et al. 2001, Brumme and Borken 1999, Dong et al. 1998, Borken and Brumme 1997, Klemedtsson and Klemedtsson 1997, MacDonald et al. 1997, Priemé and Christensen 1997, Dobbie and Smith 1996, Dobbie et al. 1996, Ambus and Christensen 1995, Dörr et al. 1993, Koschorreck and Conrad 1993

Temperate forest/woodland in North America: Borken et al. 2006, Groffman et al. 2006, McLain and Martens 2006, Suwanwaree and Robertson 2005, Teepe et al. 2004, Phillips et al. 2001, Bowden et al. 2000, Rustad and Fernandez 1998, Hudgens and Yavitt 1997, Castro et al. 1993, 1995, Goldman et al. 1995, Lessard et al. 1994, Adamsen and King 1993, Yavitt et al. 1993, Crill 1991, Steudler et al. 1989

Temperate forest/woodland in Oceania: Tate et al. 2006, Price et al. 2004

Tropical/subtropical forest: Liu et al. 2008, Yashiro et al. 2008, Zhang et al. 2008, Purbopuspito et al. 2006, Tang et al. 2006, Werner et al. 2006, Awasthi et al. 2005, Melling et al. 2005, Zhou et al. 2005, Davidson et al. 2004, Vasconcelos et al. 2004, Kiese et al. 2003, Ishizuka et al. 2002, Palm et al. 2002, Verchot et al. 2000, Weitz et al. 1998, Singh et al. 1997, Steudler et al. 1991, 1996, Castro et al. 1994a, Keller and Reiners 1994, Delmas et al. 1992, Keller et al. 1986

Boreal forest: Maljanen et al. 2006, Nakano et al. 2006, Huttunen et al. 2003, Maljanen et al. 2003, Sjögersten and Wookey 2002, Billings et al. 2000, Saari et al. 1998, Burke et al. 1997, Gulledge et al. 1997, Savage et al. 1997, Xu et al. 1996, Adamsen and King 1993, Whalen et al. 1991

2000). For example, 65 of the 70 measurements of the CH_4 uptake rate in Asia shown in Fig. 5 were taken in Japan. This may bias the flux in the other Asian temperate forests because of the high-porosity of Japanese soils due to volcanic ash deposits, although the average of CH_4 uptake rate in Japan is not significantly different from that in China and Korea.

In spite of large temperate forest area in China, only two reports on CH_4 uptake rates in China are apparently available; the values were 4.0 and 7.0 kg CH_4 ha^{-1} y^{-1} (Dong et al. 2003; Du et al. 2004). Although only two observations have been carried out in temperate forests in Oceania (Tate et al. 2006; Price et al. 2004), they have shown an annual CH_4 uptake rate of 4.9 and 10.5 kg CH_4 ha^{-1} y^{-1}, which is in the range observed in Japan and North America. There are no reports of observation of temperate forests in Australia and Eastern Europe. As mentioned in the literature (Smith et al. 2000), additional data are needed to make plausible estimates of the global terrestrial sink of CH_4.

We could not directly estimate the CH_4 uptake beneath the snow in this study. Some researchers have reported that CH_4 uptake is important throughout the snow-cover period. Sommerfeld et al. (1993) reported that the CH_4 uptake rate beneath the snow was 90% of that in the snow-free period. Morishita and Hatano (1999) also suggested that the amount of CH_4 uptake in the snow-cover season accounted for 18% of the annual amount of CH_4 uptake in Hokkaido, northern Japan.

If we adopt the value reported by Morishita and Hatano (1999), the amount of CH_4 uptake during the snow-cover period can be compensated by dividing the rate in Method 2 by 0.82. According to this

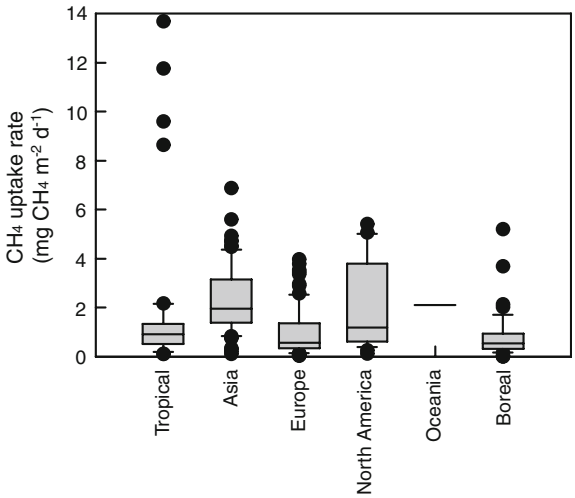

Fig. 5 Box plot for the average CH_4 uptake rate in each climatic zone. The temperate forest was divided into four geographical areas, i.e., Europe, North America, Asia and Oceania. The *boundary of the box closest to zero* means the 25th percentile; *a line in the box* means median, and *the boundary of the box farthest from zero* means the 75th percentile. The *vertical bar* means the 90th and 10th percentiles. The *closed circle* means outliers

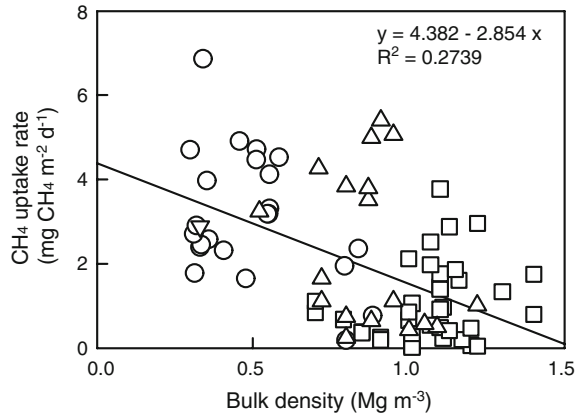

Fig. 6 Relationship between bulk density of topsoil and CH_4 uptake rate. *Open circles* are the data for Asia (this study); *open squares* are the data for Europe (Borken and Brumme 1997; Bradford et al. 2001; Brumme and Borken 1999; Butterbach-Bahl et al. 1998; Castaldi and Fierro 2005; Dong et al. 1998; Fiedler et al. 2005; Koschorreck and Conrad 1993; MacDonald et al. 1996; Merino et al. 2004; Priemé and Christensen 1997; Steinkamp et al. 2001; Teepe et al. 2004); *open triangles* are the data for North America (Borken et al. 2006; Bowden et al. 2000; Castro et al. 1993, 1994b; Crill 1991; Goldman et al. 1995; Hudgens and Yavitt 1997; Lessard et al. 1994; Phillips et al. 2001; Suwanwaree and Robertson 2005); *open triangles down* are the data for Oceania (Price et al. 2004)

calculation, the average amount of annual CH_4 uptake increased to 10.4 kg C ha^{-1}, which is close to the mean of the fluxes obtained by the original method and Method 2. Consequently, the average annual CH_4 uptake rate in this study was in a range from 9.7 to 10.9 kg CH_4 ha^{-1} y^{-1} and the plausible estimate was 10.4 kg CH_4 ha^{-1} y^{-1}.

Conclusion

We showed that the average annual CH_4 uptake rate in Japanese forest soils was somewhat higher than reported uptake rates. Our data indicate that these high CH_4 uptake rates depend on the high CH_4 oxidation rate in the topsoil (0–5 cm depth) due to the high porosity.

According to our review of the literature, the CH_4 uptake rate in temperate forests in Europe is significantly smaller than that in Asia and North America. Using this information, we determined a new global CH_4 uptake rate in temperate forests on a continental basis and obtained estimate of 5.4 Tg y^{-1} (1 SE is 1.1 Tg y^{-1}).

Table 5 Estimate of CH_4 uptake by soils in temperate forests

	Number of measures	Land area $\times 10^6$ km^2	Mean CH_4 uptake kg CH_4 ha^{-1} y^{-1}	Variance	Total flux Tg y^{-1}	SE of total flux
Europe	58	2.70	3.9	14.0	1.1	0.1
North and Central America	26	2.83	7.4	36.8	2.1	0.3
Asia	70	2.21	7.8	23.4	1.7	0.1
Oceania	2	0.70	7.7	15.7	0.5	0.2
Total	156	8.43			5.4	1.1

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