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Original article

High potential for increase in CO_2 flux from forest soil surface due to global warming in cooler areas of Japan

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Abstract – The CO_2 fluxes from the forest floor were measured using a closed chamber method at 26 sites from 26° N Lat. to 44° N Lat. in Japan. Seasonal fluctuation in CO_2 flux was found to correlate exponentially with seasonal fluctuation in soil temperature at each site. Estimate of annual carbon emission from the forest floor ranged from 3.1 to 10.6 Mg C ha^{-1}. The emission rate of soil-organic-carbon-derived CO_2, obtained by incubation of intact soil samples, correlated closely with the carboxymethylcellulase (CMCase) activity in the soil. The sum of cool-water soluble polysaccharides, hot-water soluble polysaccharides, hemicellulose, and cellulose content in the soil was greater at the sites with low CMCase activity than that at the sites with high CMCase activity. Because the sites in cooler-climate sites had a high content of easily decomposable soil organic carbon and organic litter, the potential increase in CO_2 efflux from forest floor with increasing soil temperature would be greater in cooler-climate sites.

cellulose / Japanese forest / soil organic carbon / soil respiration

Résumé – Fort potentiel d'accroissement de flux de CO_2 issu de la surface du sol forestier en relation avec le réchauffement global dans les régions fraîches du Japon. Le flux de CO_2 issu du sol forestier a été mesuré dans 26 sites, allant du 26° au 44° de latitude Nord dans l'archipel japonais, en utilisant la méthode des chambres fermées. Il a pu être mis en évidence que la fluctuation saisonnière du flux de CO_2 était corrélée de façon exponentielle avec celle de la température du sol de chacun des sites étudiés. L'estimation annelle de l'émission de carbone venant du sol variait de 3,1 à 10,6 Mg C ha^{-1}. Le taux d'émission de CO_2 obtenu par incubation d'échantillons intacts de sol est corrélé positivement avec l'activité de la carboxyméthacellulase (CMCase), dans le sol. La somme totale des polysaccharides solubles dans l'eau froide, des polysaccharides solubles dans l'eau chaude, des hémicelluloses et de la cellulose contenus dans le sol était plus grande dans les sites caractérisés par une faible activité CMCase que dans les sites avec une forte activité CMCase. Du fait que les sites en climat frais ont un contenu élevé en carbone organique du sol facilement décomposable et une litière organique, le potentiel d'accroissement du flux de CO_2 avec l'accroissement de la température du sol devrait être plus grand dans les sites à climat frais.

cellulose / forêt japonaise / carbone organique du sol / respiration du sol

1. INTRODUCTION

Carbon dioxide (CO_2) is the most important greenhouse gas, contributing to 60% of global warming [12]. The worldwide carbon stock in soils is estimated to be 1500 Pg, three times greater than that in terrestrial plants [12], and soil carbon is gradually mineralized by microorganisms to be released to the atmosphere as CO_2 gas. Generally the forest ecosystem is considered to be a CO_2 sink [33], but if the decomposition of soil carbon in the forest ecosystems is promoted by global warming, it would be doubtful whether forests could serve as CO_2 sinks. A recent study shows that soil in England and Wales lost carbon at a mean rate of 0.6% y^{-1} from 1978 to 2003 according to soil inventory data [1]. In light of global warming, the amount of carbon transferred from soil organic matter to the atmosphere is a serious concern [5].

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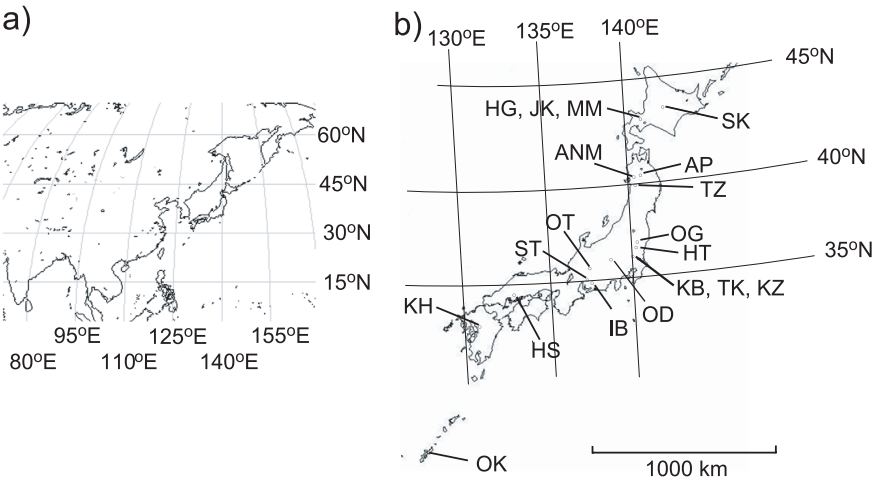

Figure 1. (a) Japan in East Asia, (b) sampling sites in Japan.

Many factors affect the decomposition of soil organic carbon in a forest ecosystem. Soil temperature often controls the seasonal fluctuation of soil respiration, which increases in summer and decreases in winter [7]. Rainfall and soil water content also affect the soil respiration, as is seen in the suppression of soil respiration by drought in Mediterranean forests in summer [15]. Besides environmental factors, the quality of organic matter is important. Soil organic carbon consists of various components with different turnover rates. Radiocarbon study indicates that the turnover times of soil organic carbon range from decades (or shorter) to millennia [31, 32]. According to these studies, the cooler the climate is, the more organic carbon with short turnover time accumulates [31]. Thus when we consider the effects of global warming on soil organic carbon, we need to take into account changes in the proportion of components with different turnover rates, as well as the direct effect of temperature on soil organic matter decomposition.

In a soil warming experiment, soil respiration was found to increase for the initial 6 years to 28% of the respiration before the experiment, but respiration was negligible from the tenth year onward, suggesting that the consumption of easily decomposable substrates within ten years serves as a limiting factor [18]. Another interpretation for the global warming effect on the soil respiration is possible: changes in soil respiration may be caused by changes in net primary production, which is related to the input of organic matter to the soil [16, 18]. Therefore, the relationship between the quality and quantity of soil carbon and CO_2 flux from the soil surface, and litter respiration remains a serious concern [10].

On the global scale, the amount of soil respirations is greater in warmer climates than in cooler climates [23]. In the tropics, vigorous plant growth and rapid decomposition of soil organic matter are responsible for the high rates of soil respiration [26]. Cold temperature inhibits organic matter decomposition, which results in the low rate of soil respiration seen in boreal forests [25]. On a continental scale, soil respiration varies from site to site. It does not relate to mean annual temperature over a wide range of European forest ecosystems [9, 15]. Davidson et al. [5] suggest that this insensitivity to temperature results from a great accumulation of easily decomposable substrates in cool climates. However, few studies had been conducted to examine how soil respiration varies with latitude. To estimate the soil respiration rate on a global scale, observation at different latitude at another longitude would be useful.

Much soil respiration research has been conducted on forest ecosystems in Japan, but different researches have used different methods (e.g., alkaline absorption, dynamic chamber), which raises the problem of comparing data among sites. The objectives of this research are (1) to compare soil respiration in various forest ecosystems at different latitude in Japan, from 26° N to 44° N Lat., using a single method, and (2) to analyze the relationship between CO_2 flux from the soil and the qualities of soil organic carbon. This study promises to contribute to understanding of Japan-wide CO_2 emission from the soil surface and the characteristics of soil organic carbon in Japanese forests.

2. MATERIALS AND METHODS

2.1. Site description

We established 26 forested plots for CO_2 flux measurement through the Japanese islands from 26° N to 44° N Lat. (Fig. 1 and Tab. I). These are mainly humid temperate forests, with four exceptions: 1 subtropical forest (OK) and 3 sub-alpine coniferous forests (SK, OD1 and OD2). The mean annual soil temperatures of these sites range from 4 to 22 °C. The mean annual rainfall for the last ten years at the meteorological station nearest each site ranged from 1200 to 3500 mm (1630 mm on average) (Japan Meteorological Agency, Automated Meteorological Data Acquisition System: http://www.data.kishou.go.jp/). 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 central sites (OG, HT, KB, TK, KZ, ST and IB) are sometimes covered with snow for a few weeks in winter. The ages of trees at all plantations were greater than 20 years. Four soil types (Cambisol, Andosol, Podzol and Alisol) exist at the study sites, and most sites are affected by

Table I. General Information of the Sites.

Site	Lat.	Long.	Elev. (m)	Vegetation[a]	Forest type	Soil type[b]	Annual rainfall[c]	Avg. soil temp. (°C)	Flux observation period	Number of samplings
SK	43° 40'	143° 06'	1000	PJ, AS	Natural	Podzol	1418	4.1[e]	Sep 99 – Oct 01	8
JK	42° 58'	141° 10'	322	AS	Planted	Cambisol	1268	7.3[e]	Jun 99 – May 01	6
MM	42° 56'	141° 16'	440	AS	Planted	Cambisol	1268	6.4[f]	Jun 99 – Sep 99	4
HG1	42° 59'	141° 23'	240	BP, QM	Natural	Andosol	1167	7.6[f]	Jun 98 – Sep 99	12
HG2	42° 59'	141° 23'	260	BP, QM	Natural	Andosol	1167	7.5[f]	Jun 98 – Sep 99	11
HG3	42° 59'	141° 23'	175	BP, QM	Natural	Andosol	1167	8.3[e]	Jun 98 – Aug 00	6
AP	39° 59'	140° 54'	825	FC	Natural	Andosol	1207	6.9[e]	Jun 00 – Nov 01	13
ANM	39° 59'	140° 24'	200	CJ	Planted	Cambisol	2006	9.4[f]	Jun 01 – Nov 02	14
TZ	39° 46'	140° 43'	350	CJ	Planted	Andosol	2188	9.6[e]	Jul 00 – May 02	13
OG1	36° 56'	140° 35'	650	FC, FJ	Natural	Andosol	1948	10.6[e]	May 95 – Mar 02	30
OG2	36° 56'	140° 35'	650	FC, FJ	Natural	Cambisol	1948	10.6[e]	Jul 95 – Mar 98	13
OG3	36° 56'	140° 35'	650	CJ	Natural	Andosol	1948	9.5[e]	Jun 97 – Mar 02	18
OG4	36° 56'	140° 35'	650	QS, CA	Deforested	Cambisol	1948	ND[g]	Nov 96 – Dec 97	6
HT	36° 35'	140° 35'	380	CA	Mixed[d]	Cambisol	1371	12.1[f]	Jul 97 – May 98	6
KB1	36° 18'	140° 09'	470	CA, QM	Mixed[d]	Cambisol	1310	11.1[f]	Aug 97 – Jun 02	23
KB2	36° 19'	140° 09'	250	CO	Planted	Cambisol	1310	12.0[e]	Apr 99 – Jun 02	19
TK	36° 10'	140° 11'	330	CJ	Planted	Andosol	1310	12.2[f]	May 95 – Nov 95	6
KZ	36° 00'	140° 08'	22	CO	Planted	Andosol	1203	14.0[f]	Feb 95 – Aug 95	5
OT	35° 55'	137° 19'	1350	CO	Planted	Andosol	3502	6.4[f]	Aug 00 – Dec 01	13
OD1	35° 51'	138° 39'	2090	AV	Natural	Podzol	1365	4.2[e]	Jun 99 – Sep 01	14
OD2	35° 51'	138° 39'	2080	LK	Planted	Podzol	1365	5.2[e]	Jun 99 – Sep 01	14
ST	35° 14'	137° 08'	630	CO	Planted	Cambisol	1528	11.2[e]	Jul 00 – Dec 01	14
IB	35° 12'	137° 34'	1010	CO	Planted	Cambisol	1972	9.3[e]	Jul 00 – Dec 01	14
HS	34° 24'	132° 43'	240	PD	Natural	Cambisol	1513	15.1[f]	Oct 01 – Dec 01	3
KH	33° 05'	130° 26'	165	CO, CJ	Planted	Cambisol	2072	14.2[e]	May 00 – Mar 03	35
OK	26° 31'	127° 59'	100	CC	Natural	Alisol	2131	21.5[e]	Apr 99 – Jan 02	7

[a] AV: *Abies veitchii*, AS: *Abies sachalinensis*, BP: *Betula platyphylla*, CA: *Carpinus* spp., CC: *Castanopsis cuspidata*, CJ: *Cryptomeria japonica*, CO: *Chamaecyparis obtusa*, FC: *Fagus crenata*, FJ: *Fagus japonica*, LK: *Larix kaempferi,* CJ: *Cryptomeria japonica*, CO: *Chamaecyparis obtusa*, FC: *Fagus crenata*, FJ: *Fagus japonica*, LK: *Larix kaempferi,* PD: *Pinus densiflora*, PJ: *Picea jezoensis*, QM: *Quercus mongolica*, QS: *Quercus serrata.*
[b] WRB classification (ISSS Working Group RB, 1998).
[c] 1993–2002 at the nearest meteorological station of Japan Meteorological Agency.
[d] Unsuccessful afforestation (overgrown by natural vegetation).
[e] Average soil temperature through a year measured with a thermorecorder at 1-h intervals.
[f] Estimation; based on the mean annual air temperature at the nearest meteorological station and the elevation of the site.
[g] ND: cannot be estimated because the daily fluctuation of flux did not correlate with soil temperature due to deforestation.

volcanic ash deposition to some extent even though the soil is not Andosol. The general soil properties are shown in Table II.

2.2. Flux measurement

CO_2 flux was measured by static chamber method [24]. Three or five stainless-steel chambers (40 cm in diameter, 15 cm in length) were inserted in the soil to a depth of at least 1 cm at each site. Each chamber was fixed at its location throughout the observation period. For CO_2 flux measurement, the chamber was covered with a PVC lid with a sampling port and an air bag to equalize the air pressure in the chamber. We took gas samples from the chamber using a disposable syringe at 0, 10, 20 and 40 min elapsed after the chamber was covered with a lid. Each gas sample was filled into a glass vial with a butyl rubber top that had been evacuated beforehand in the laboratory. The CO_2 gas concentration was determined using a gas chromatograph equipped with a thermal conductivity detector (Shimazu GC-14B-TCD, Japan). A 5-mL gas sample was used for analysis. Standard calibration was made using standard gases of 310 and 4130 μL CO_2 L^{-1} (Sumitomo Seika Chemicals Co., Japan). We calculated fluxes using a non-linear model [11], in which the chamber volume was corrected according to the air pressure for the altitude of the plot. The CO_2 fluxes were measured monthly, avoiding a rainy

Table II. Soil characteristics of the surface 5 cm of soil.

Site	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		Microbial biomass C μg C g^{-1}	Soil texture		
						NH_4-N μg g^{-1}	NO_3-N μg g^{-1}		Sand (%)	Silt (%)	Clay (%)
SK	4.2	0.78	86	4.6	ND[a]	17.2	2.0	1305	51.3	27.8	20.9
JK	5.1	0.45	50	3.1	ND[a]	ND[a]	ND[a]	ND[a]	50.0	32.6	17.4
MM	5.3	0.59	55	4.0	0.46	25.0	2.3	ND[a]	56.8	34.0	9.2
HG1,2	6.0	0.68	78	5.7	0.55	19.7	1.7	534	59.7	25.1	15.2
HG3	6.2	1.08	104	5.6	0.36	11.8	0.5	1704	ND[a]	ND[a]	ND[a]
AP	4.5	1.17	129	8.7	0.41	21.5	7.8	3119	16.3	40.2	43.4
ANM	5.2	ND[a]	300	12.5	ND[a]	ND[a]	ND[a]	ND[a]	11.9	53.5	34.6
TZ	5.8	1.23	140	8.6	0.33	21.7	12.9	1702	13.5	75.4	11.1
OG1	4.9	1.67	230	13.0	0.33	13.8	15.3	2262	ND[a]	ND[a]	ND[a]
OG2	4.8	0.78	54	4.0	0.51	9.0	1.2	1524	ND[a]	ND[a]	ND[a]
OG3	4.5	1.04	162	10.4	0.35	ND[a]	ND[a]	ND[a]	30.9	20.1	49.0
OG4	4.8	0.64	94	5.6	0.58	10.6	6.4	2021	63.1	22.5	14.4
HT	4.5	0.50	48	3.1	0.55	13.5	18.5	ND[a]	40.9	36.5	22.6
KB1	4.6	0.94	125	10.2	0.34	10.0	9.2	ND[a]	62.6	18.3	19.2
KB2	ND[a]	1.32	148	9.1	0.30	ND[a]	ND[a]	ND[a]	ND[a]	ND[a]	ND[a]
TK	4.4	1.45	169	11.0	0.31	14.9	48.8	ND[a]	ND[a]	ND[a]	ND[a]
KZ	ND[a]	ND[a]	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	1700	ND[a]	ND[a]	ND[a]
OD1	3.7	1.18	212	11.6	0.32	14.9	14.2	3275	43.1	20.7	36.2
OD2	4.0	0.62	132	7.5	0.55	13.6	9.3	2361	59.6	16.5	23.9
ST	4.2	0.45	24	1.7	0.79	9.7	1.9	634	26.1	20.2	53.6
IB	4.8	1.04	80	4.6	0.51	20.4	5.3	1123	25.3	21.6	53.1
HS	4.3	0.36	71	3.4	0.88	13.1	0.3	1008	74.3	12.7	13.0
KH	4.5	0.61	42	2.7	0.84	13.8	0.1	1157	28.3	37.5	34.2
OK	4.9	0.25	50	2.4	0.80	8.8	0.4	1632	41.6	38.9	19.4

[a] Not determined.

day. When snow covered the whole surface of the chamber, we did not take gas samples. While collecting gas samples, we measured the air temperature 1 m above the ground and the soil temperature at 5 cm depth. Soil temperature at 5 cm depth was also recorded hourly using a data logger (TR-71S or TR-52, T & D Co., Japan). At sites without a temperature data logger, hourly soil temperature was estimated from the air temperature obtained from the nearest meteorological station (Japan Meteorological Agency, Automated Meteorological Data Acquisition System) using the relationship between air temperature and soil temperature measured on sampling days. We defined an "integrated soil temperature" as the sum of the daily average soil temperatures for one year.

2.3. Soil analysis

Soils for chemical analysis were sampled from the depths of 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. The soil total carbon and nitrogen contents were measured using an NC analyzer (NC-800, Sumitomo Chemical Co., Japan). The inorganic NH_4 and NO_3 in the extractant of 10 g fresh soil shaken with 100 mL 2M KCl for 1 h were determined using a flow-injection analyzer (Aquatec 5400, Tecator Co., Sweden). Soil water content was calculated by the weight difference before and after oven drying at 105 °C for 24 h. We determined the content of wax, cool-water-soluble polysaccharides, hot-water-soluble polysaccharides, hemicellulose, cellulose, and lignin in the soils of ten sites (HG3, AP, TZ, OD1, OD2, IB, ST, KH, HS and OK). The wax was extracted using a Soxhlet-extraction system with 1:1 benzene-ethanol solution for 24 h and weighed after the solvent was evaporated. After the Soxhlet-extraction, cool-water-soluble polysaccharides, hot-water-soluble polysaccharides, hemicellulose and cellulose were obtained by sequential extraction using cool water, hot water, 2% HCl solution, and 72% H_2SO_4 solution, respectively, and lignin was obtained in the residue [29]. The contents in each fraction, except lignin, were expressed as the sum of pentose and hexose [20]. The pentose content was determined by orcinol method [19], and the hexose content was determined by anthrone method [4]. Once all the extraction were complete, carbon and nitrogen contents of the residue were measured using an NC analyzer and the lignin content was calculated using this equation: lignin content = carbon content × 1.724 – nitrogen content × 6.25. The microbial biomass carbon was measured

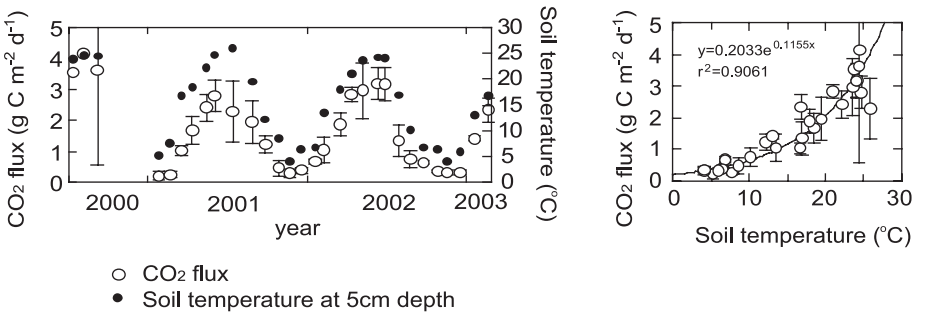

Figure 2. Example of seasonal fluctuation of CO_2 flux (left) and the correlation between CO_2 flux and soil temperature (right) at KH.

by chloroform fumigation extraction method [34] using a TOC analyzer (TOC-5000, Shimazu Co., Japan). Carboxymethylcellulase activity (CMCase) was determined by the difference in the reducing sugar contents in the sample and in a control solution [21]. The reducing sugar contents were determined by Somogyi-Nelson method [28]. The activity of phosphomonoesterase was determined by colorimetric method [30] with a minor modification [13]. The particle size distribution was determined by pipette sampling method [6].

2.4. Soil core incubation

Intact soil cores with a volume of 100 mL (5 cm in diameter, 5.1 cm in height) were collected from the soil depths corresponding to the soil sampling depth at each plot. Triplicate samples were collected for each depth. We incubated soil cores to evaluate the potential of CO_2 emission of the soils at the ten sites (HG3, AP, TZ, KB2, OD1, OD2, IB, ST, KH and OK) by the following method [14]. An intact soil core was placed in a 500-mL incubation jar at 25 °C and stopped with a butyl rubber stopper. The gas in the headspace was sampled 4 h and 24 h after closure. The CO_2 concentration in the headspace was preliminarily found to show a linear increase during this incubation period. The emission rate of CO_2 from the soil core was calculated using the slope of a line showing the rate of increase in CO_2 concentration with time. All data are the means of triplicate samples. We defined the emission potential of CO_2 derived from soil organic carbon decomposition (hereafter SOC-CO_2) as the sum of the emission rates at 0–5 cm, 5–10 cm and 10–15 cm depths obtained by incubation method.

3. RESULTS

3.1. CO_2 flux from the forest floor

The CO_2 flux from the forest floor fluctuated seasonally, showing maximum in summer and minimum in winter. The CO_2 fluxes during the observation period ranged from 0.08 to 5.89 g C m^{-2} d^{-1} (Tab. III). The fluxes correlated exponentially with the soil temperature at 5 cm depth at most sites (an example is shown in Fig. 2), and the flux can be expressed by the following equation:

$$\text{Flux (gC m}^{-2}\text{ d}^{-1}) = A\, e^{BT} \quad (1)$$

where T is the soil temperature at 5 cm depth (°C), and A and B are constants for each site. A is the CO_2 flux at 0 °C and B is the parameter of temperature dependency (if B is larger than 0.069, then Q_{10} is greater than 2). To compare the CO_2 flux under the same temperature at all sites, the CO_2 flux at 15 °C calculated using the (Eq. (1)) was used. The fluxes correlated negatively with the integrated soil temperature (Fig. 3).

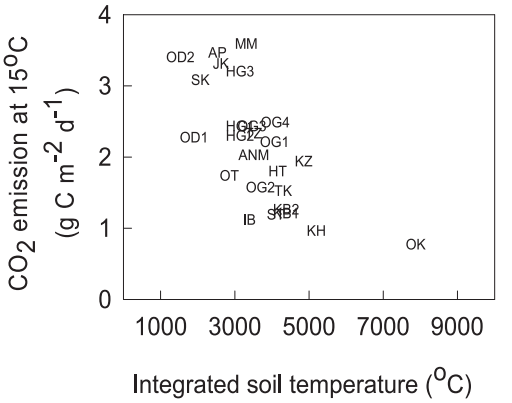

Figure 3. Relationship between integrated soil temperature and CO_2 flux at 15 °C calculated using the parameter in Table III.

Annual CO_2 flux from the forest floor at each site was estimated by the sum of hourly CO_2 flux calculated by equation (1), using the data logger records of hourly soil temperature at 5 cm depth on the site (Tab. III). Because the soil temperature and CO_2 flux at KZ did not show a close relationship, we did not calculate the annual CO_2 efflux at KZ. The estimated CO_2 flux from the forest floor ranged from 3.1 to 10.6 Mg C ha^{-1} y^{-1} (Tab. III). A correlation between integrated soil temperature and CO_2 efflux was not found (Fig. 4). The average of annual CO_2 efflux at the northern sites (SK, JK, MM, HG, AP, ANM, TZ and OG; the mean and standard deviation were 6.82 ± 1.18) was significantly greater than at southern sites (HT, KB, TK, OT, OD, ST, IB, HS, KH and OK; the mean and standard deviation were 4.91 ± 2.06) (p = 0.009 in student's t-test). To compare our data with global-scale observations, the estimated CO_2 flux was calculated by the following equation [25]:

$$\text{EVOL} = -0.242 \times (\text{LAT}) + 17.215 \quad (2)$$

where EVOL (Mg C ha^{-1} y^{-1}) is CO_2 flux from the forest floor and LAT (°) is the north latitude of the site. The flux rates

Table III. Estimates of annual CO_2 emission rate from the relationship between soil temperature and CO_2 flux (rate 1) and annual CO_2 emission rate estimated by Schlesinger's equation (rate 2).

Site	Avg. soil temp.	CO_2 flux range (g C m^{-2} d^{-1})		Regression parameter[a]			Annual CO_2 emission rate	
							Rate 1	Rate 2
	°C	min	max	A	B	r^2	(Mg C ha^{-1})	(Mg C ha^{-1})
SK	5.70	1.22	3.91	0.795	0.090	0.937	5.71	6.65
JK	8.70[b]	1.69	5.53	0.973	0.082	0.786	7.66	6.82
MM	9.00[b]	2.17	5.49	1.005	0.085	0.996	9.27	6.83
HG1	9.00[b]	0.96	4.36	0.541	0.100	0.832	6.32	6.82
HG2	9.00[b]	0.83	4.61	0.579	0.092	0.862	6.52	6.82
HG3	9.00[b]	2.07	4.96	0.894	0.085	0.897	8.51	6.82
AP	8.90	0.68	4.71	0.546	0.123	0.848	6.69	7.54
ANM	9.56[b]	1.47	3.10	0.845	0.054	0.707	6.22	7.54
TZ	9.56	0.81	5.42	0.419	0.114	0.916	7.02	7.59
OG1	11.14[b]	0.13	5.60	0.268	0.141	0.783	6.62	8.28
OG2	10.09[b]	0.33	4.73	0.238	0.126	0.979	6.76	8.28
OG3	9.47[b]	0.08	4.65	0.222	0.137	0.813	4.57	8.28
OG4	11.19[b]	0.57	5.82	0.322	0.136	0.907	6.80	8.28
HT	11.80[b]	0.19	4.19	0.190	0.150	0.860	5.79	8.37
KB1	11.80[b]	0.10	3.41	0.184	0.129	0.851	4.61	8.43
KB2	11.80	0.35	1.78	0.463	0.068	0.602	4.26	8.43
TK	11.77[b]	0.83	2.22	0.689	0.053	0.697	5.83	8.42
KZ	13.40[b]	0.50	2.89	0.832	0.056	0.347	ND[c]	8.50
OT	7.80[b]	0.33	2.74	0.268	0.125	0.968	3.56	8.52
OD1	5.19	0.55	5.89	0.560	0.094	0.802	3.60	8.54
OD2	4.18	0.68	2.91	0.552	0.121	0.693	4.35	8.54
ST	10.83	0.71	1.99	0.564	0.050	0.586	4.05	8.69
IB	8.95	0.50	1.92	0.323	0.083	0.805	3.06	8.70
HS	ND[c]	0.78	1.44	ND[c]	ND[c]	ND[c]	ND[c]	ND[c]
KH	14.23	0.22	4.18	0.140	0.129	0.906	4.29	9.20
OK	21.99	0.76	2.70	0.062	0.168	0.901	10.57	10.80

[a] Regression parameter of the equation: $[\text{flux}] = A \times e^{B[\text{SoilTemperature}]}$.
[b] Estimated using the data of the nearest meteorological station (http://www.data.kishou.go.jp/).
[c] Not determined.

estimated using equation (2) were almost the same as those measured at the sites north of 39° N (north of TZ), but were higher than those measured at sites south of 39° N.

3.2. Soil organic components

The sum of cool-water-soluble polysaccharides and hot-water-soluble polysaccharides, hemicellulose and cellulose ranged from 790 to 2700 g m^{-2} in the soil from 0 to 15 cm depth. This was 19.4% of the total soil organic matter on average (Tab. IV). Of these components, the hemicellulose content was the highest (66.7% of the sum of polysaccharides, hemicellulose and cellulose on average). The hemicellulose content (14.2% on average) was two to nine times greater than the cellulose content. Lignin content ranged from 24.4 to 56.6% of total soil organic matter. The ratio of cellulose to hemicellulose to lignin was 1:5:17 on average, which is remarkably different from that in plant materials (e.g., 2:1:1 in woody xylem, and 1:1:2 in leaves) and litter (nearly the same ratio as in leaves [3]).

3.3. Soil enzyme activities

CMCase is an endo-β-glucanase (EC 3.2.1.4), that is used as an index of microbial activity in cellulosic material decomposition [27]. CMCase activity ranged from 4.5 to 24.0 g-glucose d^{-1} per square meter in the soil from 0–15 cm depth (Tab. V). The activity of phosphomonoesterase correlated with that of CMCase (Tab. V, $r = 0.716$, $n = 9$, $p < 0.05$ in Pearson's correlation test), suggesting that these enzyme activities

Table IV. Soil organic matter, wax, polysaccharides, hemicellulose, cellulose and lignin contents in topsoil[a].

Site	Organic matter[b]	Wax	Soil cellulosic materials									Lignin
			Cool-water extracted		Hot-water extracted		Hemicellulose		Cellulose		Total	
			Hexose[c]	Pentose[d]	Hexose[c]	Pentose[d]	Hexose[c]	Pentose[d]	Hexose[c]	Pentose[d]		
	(kg m^{-2})	(g m^{-2})	(g m^{-2})	(g m^{-2})	(g m^{-2})	(g m^{-2})	(g m^{-2})	(g m^{-2})	(g m^{-2})	(g m^{-2})	(g m^{-2})	(g m^{-2})
HG3	8.2	252	37	7	74	29	510	195	108	16	980	2210
AP	11.0	385	23	7	233	63	1640	483	222	26	2700	4595
TZ	13.0	157	19	6	152	41	1210	455	226	42	2150	7350
OD1	18.9	635	22	6	422	160	945	318	152	20	2050	5450
OD2	15.8	525	22	6	338	116	760	243	125	17	1630	4030
ST	4.2	207	45	17	114	45	660	267	282	39	1470	1645
IB	8.9	272	25	8	116	37	1010	388	285	37	1900	3430
HS	7.1	385	26	8	188	82	378	143	207	25	1060	1740
KH	6.4	426	55	20	244	71	1200	385	235	35	2250	3200
OK	5.9	422	17	4	113	44	334	134	126	17	790	1905

[a] Total amount in the soil from 0 to 15 cm depth.
[b] Carbon content × 1.724.
[c] Equivalent to glucose weight.
[d] Equivalent to xylose weight.

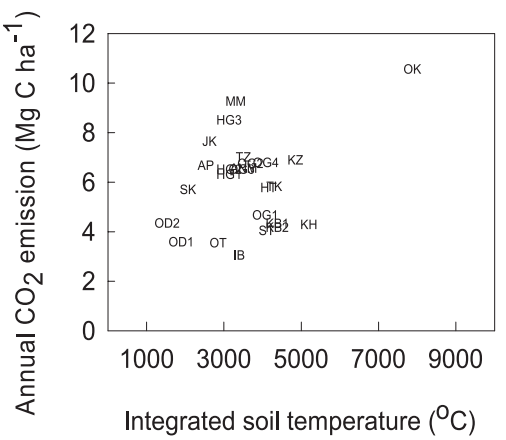

Figure 4. The relationship between integrated soil temperature and annual CO_2 emission from soil surface.

can be used as an indicator of total microbial activity for decomposing soil organic matter in Japanese soils.

3.4. CO_2 emission potential for soil

The CO_2 emission rates (mg C d^{-1}) from incubated soil cores ranged from 0.76 to 3.42 at 0–5 cm depth, from 0.28 to 0.96 at 5–10 cm depth, and from 0.26 to 1.06 at 10–15 cm depth. Approximately 60% of CO_2 emission was derived from the uppermost 5-cm layer on average. The emission potential of SOC-CO_2 correlated positively with CMCase activity and correlated negatively with the cellulose content (Fig. 5). The other soil constituents did not correlate significantly with the emission potential of SOC-CO_2 ($p > 0.05$ in Pearson's correlation test).

Table V. Enzyme activities in topsoils[a].

Site	CMCase (g d^{-1})[b]	Phospho-monoesterase (mol h^{-1})
HG3	ND[c]	ND[c]
AP	7.2	2.7
TZ	8.4	1.6
OD1	6.9	3.7
OD2	14.9	2.3
ST	6.2	3.0
IB	4.5	4.5
HS	24.0	7.2
KH	9.3	2.9
OK	20.3	9.3

[a] Total amount in the soil from 0 to 15 cm depth per square meter.
[b] Equivalent to glucose weight.
[c] Not determined.

4. DISCUSSION

We did not find that the CO_2 flux from the soil surface tended to decrease with the increase of latitude, as was reported by Schlesinger [25] (Tab. III). If we exclude OK from the analysis, we see the opposite trend: The average CO_2 efflux was higher at higher latitudes. This means that heterotrophic respiration (from litter and soil organic matter decomposition) and/or autotrophic respiration (from roots) was greater

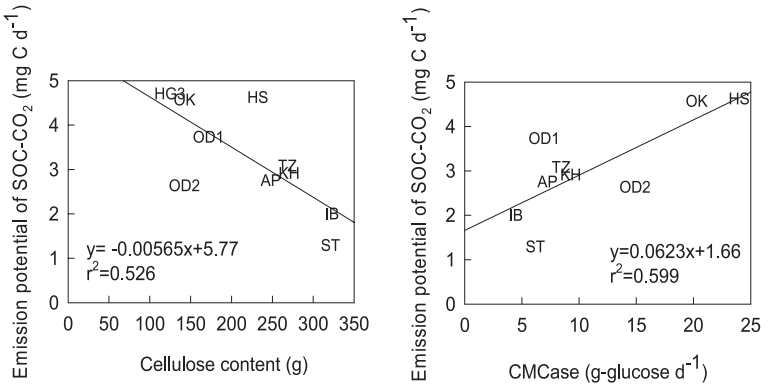

Figure 5. Relationship between SOC-CO_2 emission potential at 25 °C and cellulose content (left) and CMCase (right). Both cellulose contents and CMCase are the sum per square meter at 15 cm depth.

in cooler climates than in warmer climates. We calculated the annual CO_2 emission from soil organic carbon (SOC-CO_2) by equation (1) using the hourly soil temperature at 5 cm depth at the site, parameter *B* in Table III, and CO_2 emission from soil core incubation. The annual rate of SOC-CO_2 correlated exponentially with the integrated soil temperature (data not shown). In addition as the temperature dependency of SOC-CO_2 emission is greater in cooler climates than in warmer climates [17], the SOC-CO_2 in cooler climates is expected to be smaller than the value estimated above. Although the estimated annual amount of SOC-CO_2 was just an approximation, the SOC-CO_2 in cooler climate is expected to be smaller than that in warmer climates. Hence it is possible that the trend in which the average CO_2 efflux was higher at higher latitudes is caused by the high contribution of litter decomposition and/or root respiration to the total CO_2 efflux from forest floor in the cooler climates. Although we did not measure root mass or respiration in the soil, it is unlikely that root respiration is higher in cooler climates than in warmer climates, because gross primary productivity controls the root respiration [15] and gross primary production in cooler climates tends to be low [2]. Consequently, because the accumulated mass of the litter layer is greater in cooler climates than in warmer climates, it is plausible that the CO_2 emission from litter decomposition, which is controlled by the quantity and quality of litter and microbial activity rather than by the temperature, contributed to the opposite trend in which the average CO_2 efflux was higher at higher latitudes. Another possible explanation for the trend in which the average CO_2 efflux was higher at higher latitudes is the suppression of CO_2 flux in southern Japan. Those sites with a relatively lower coefficient of determination in equation (1) tend to have a low temperature dependency and they tend to distribute more southerly among our experimental sites. For example, the value of parameter *B* in equation (1) was low at KB2, TK, KZ and ST (Tab. III). This low temperature dependency seems to depend on the fact that in summer the CO_2 flux does not increase as much as the increase estimated by soil temperature, because of the low soil water content (Sakata, unpublished data) – a phenomenon seen in Mediterranean forest [7, 15]. This variation in soil water content among the sites, caused by the change in balance

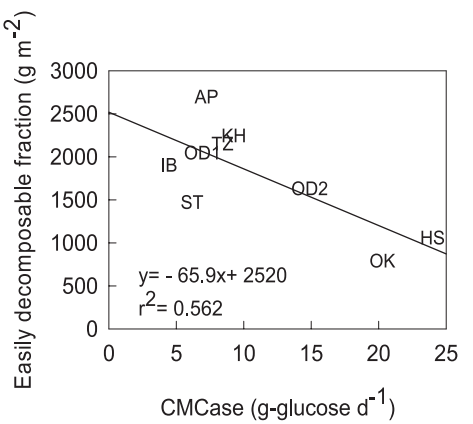

Figure 6. Correlation between the easily decomposable fraction (the sum of cool-water-soluble polysaccharides, hot-water-soluble polysaccharides, hemicellulose, and cellulose) and CMCase activity.

of rainfall and evapotranspiration, could also contribute to the opposite trend to some extent.

The quality of organic carbon is a crucial factor for determining CO_2 emission from the soil. The ratio of cellulose to hemicellulose to lignin was 1:5:17 for 0–15 cm depth. The low proportion of cellulose indicates that cellulose has already been decomposed by microorganisms due to its labile characteristics. This is consistent with our finding that CMCase activity correlates negatively with the amount of easily decomposable fractions (i.e. sum of cool-water-soluble polysaccharides and hot-water- soluble polysaccharides, hemicellulose and cellulose) (Fig. 6). Microorganisms seem to consume these fractions actively. This also suggests that the residual amount of easily decomposable fractions can be used as an inverse indicator of the emission potential of SOC-CO_2 and that emission of SOC-CO_2 is not controlled by the substrate availability of the soil organic carbon.

Global warming is increasing soil temperature, which will promote CO_2 emission from the soil surface by accelerating the decomposition of soil organic matter and litter. In the warmer-climate area, however, the low concentration of easily decomposable organic carbon in the soil (e.g., HS and OK

in Fig. 6) and the small amount of soil organic matter suggest that increases in CO_2 emission will be limited despite soil temperature increases. The hypothesis that increases in CO_2 flux are limited by the rapid decay of easily decomposable organic carbon is consistent with previous reports [18, 22]. In addition, it is important to identify the substrate that directly correlates to potential of SOC-CO_2 emission, because the abundance of that substrate helps us to predict how large the global warming-related increase in CO_2 emission will be and how long it will continue. We suggest the possible substrate is cellulose and/or the sum of cool-water-soluble polysaccharides and hot-water-soluble polysaccharides, hemicellulose and cellulose in the soil. Then it is needed to determine the applicability of the index to other latitude gradients and vegetation-soil patterns.

The sites with lower integrated soil temperature had high CO_2 flux at 15 °C (Fig. 3), which suggests that cool-climate areas have high potential for CO_2 emission if the temperature increases. In cool-climate areas, large stocks of easily decomposable organic carbon seem to be accumulated not only in the soil but also in the organic layer. Since the increase in temperature is projected to be greater at higher latitudes [8], the effects of global warming on the CO_2 efflux from the forest floor is a particularly serious concern in cooler climates, such as found at high latitudes and at high altitudes. In contrast to warmer-climate areas, CO_2 emission is expected to be high for a considerable period in cool-climate areas if the soil temperature increases from global warming.

The carbon concentration in the soil layer deeper than 15 cm was lower than that in the surface 15-cm soil layer. This study did not take the deeper soil layer into account in evaluating the emission of SOC-CO_2, although the soil carbon in the deeper layer may be influenced by global warming in the long term. Because the type of vegetation on the site has changed over a long time, the carbon source and the characteristics in the deeper layer might differ from those in the surface layer. This discrepancy may make it difficult to estimate the influence of the global warming on the decomposition of the soil carbon by simple characterization of soil organic matter. The decomposition of carbon stocks in deeper soil layers should be evaluated in the future.

5. CONCLUSION

The CO_2 flux from the forest floor within each forest showed an exponential correlation with the soil temperature at 5 cm depth at 26 sites in Japan. The annual carbon flux ranged from 3.1 to 10.6 Mg C ha^{-1}. The southern Japanese forest showed lower CO_2 efflux than that the northern forests, except for the southernmost subtropical forest. The CO_2 emission potential derived from the decomposition of soil organic carbon correlated positively with CMCase activity, and correlated negatively with cellulose content in the soil. This suggests that emission of SOC-CO_2 is not controlled by the substrate availability in Japanese forests. Our results also suggest that the period in which the CO_2 flux from the forest floor would be elevated by global warming would vary with respected to the amount of easily decomposable organic carbon in the soil. The period of increasing CO_2 flux will be somewhat longer in the cooler-climate areas than in warmer-climate areas due to the large accumulation of easily decomposable organic carbon in the soil. This may make cooler-climate regions more sensitive to CO_2 emissions from forest floor that result from global warming.

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