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Effects of multiple environmental factors on CO_2 emission and CH_4 uptake from old-growth forest soils

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Abstract. To assess contribution of multiple environmental factors to carbon exchanges between the atmosphere and forest soils, four old-growth forests referred to as boreal coniferous forest, temperate needle-broadleaved mixed forest, subtropical evergreen broadleaved forest and tropical monsoon rain forest were selected along eastern China. In each old-growth forest, soil CO_2 and CH_4 fluxes were measured from 2003 to 2005 applying the static opaque chamber and gas chromatography technique. Soil temperature and moisture at the 10 cm depth were simultaneously measured with the greenhouse gas measurements. Inorganic N (NH_4^+-N and NO_3^--N) in the 0–10 cm was determined monthly. From north to south, annual mean CO_2 emission ranged from 18.09 ± 0.22 to 35.40 ± 2.24 Mg CO_2 ha^{-1} yr^{-1} and annual mean CH_4 uptake ranged from 0.04 ± 0.11 to 5.15 ± 0.96 kg CH_4 ha^{-1} yr^{-1} in the four old-growth forests. Soil CO_2 flux in the old-growth forests was mainly driven by soil temperature, followed by soil moisture and NO_3^--N. Temperature sensitivity (Q_{10}) of soil CO_2 flux was lower at lower latitudes with high temperature and more precipitation, probably because of less soil organic carbon (SOC). Soil NO_3^- accumulation caused by environmental change was often accompanied by an increase in soil CO_2 emission. In addition, soil CH_4 uptake decreased with an increase in soil moisture. The response of soil CH_4 flux to temperature was dependent upon the optimal value of soil temperature in each forest. Soil NH_4^+-N consumption tended to promote soil CH_4 uptake in the old-growth forests, whereas soil NO_3^- accumulation was not conducive to CH_4 oxidation in anaerobic condition. These results indicate that soil mineral N dynamics largely affects the soil gas fluxes of CO_2 and CH_4 in the old-growth forests, along with climate conditions.

1 Introduction

It is generally thought that old-growth forests cease to accumulate carbon (C) with the equal of mean CO_2 emission from heterotrophic respiration to mean CO_2 sequestration as net primary production (Odum, 1969). Recently, some studies have suggested that old-growth forests can continue to sequester C and serve as a global CO_2 sink (Zhou et al., 2006; Luyssaert et al., 2008). Most of the sequestered CO_2 is stored as slowly decomposing organic matter in litter and soil (Zhou et al., 2006). As an important process of C cycling, soil CO_2 and CH_4 fluxes are driven by many environmental factors, including availability and amount of C substrates, temperature, precipitation and soil water content, redox potential and aeration, diffusion, soil texture, soil pH, salinity, sodicity and acidity, ion deficiencies and toxicities and elevated CO_2 and atmospheric N deposition (Dalal and Allen, 2008). Therefore, assessing contribution of multiple environmental factors is critical to model or to predict C exchanges between the atmosphere and forest soils.

In the past two decades, studies on responses of soil C fluxes to climate change and N deposition in forests mostly focused on manipulative experiments such as warming (Melillo et al., 2002), throughfall exclusion (Davidson et al., 2004; Borken et al., 2006; Sotta et al., 2007), and N addition (Bowden et al., 2004; Micks et al., 2004; Mo

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et al., 2008; Zhang et al., 2008). However, manipulative experiments could be incompletely equal to natural environmental changes due to transient change of activities of plant roots and soil microorganisms, which could draw various conclusions (Corre et al., 2007; Kleja et al., 2008). For example, addition of N to forest soils may increase (Tessier and Raynal, 2003; Micks et al., 2004), decrease (Chantigny et al., 1999; Bowden et al., 2004) or have no effect on (Prescott et al., 1999; McDowell et al., 2004) soil CO_2 and CH_4 fluxes. Also, the responses of soil respiration to warming included both promotion (Bergner et al., 2004) and acclimation (Luo et al., 2001; Melillo et al., 2002). To our knowledge, only few reports are available on evaluating the combination effects of multiple environmental factors on CO_2 and CH_4 fluxes from old-growth forest soils under non-manipulation conditions.

Environmental gradient method, which can deal with a gradual and continuous change in time and space, is widely applied in studying the responses of C and N processes to climate change (Corre et al., 2007; Kleja et al., 2008). In eastern China, mean annual temperature varies from −7°C in the cold temperate continent monsoon climatic zone of the north to over 26°C in the equatorial monsoon climatic zone of the south (Yu et al., 2008). Mean annual precipitation decreases from about 2200 mm in the south to less 230 mm in the north (Yu et al., 2008). Zonal forest ecosystems, from the tropical rain forest in the south to the boreal coniferous forest in the north, provide a unique research platform to investigate the effects of multiple environmental factors on soil CO_2 and CH_4 fluxes in old-growth forests.

In this paper, we analyzed three-year data on soil CO_2 and CH_4 fluxes, soil temperature, soil moisture, and mineral N concentrations which were measured in four old-growth forests in eastern China. Our specific aims are (Eq. 1) to compare the difference of soil CO_2 and CH_4 fluxes in different forests in eastern China; (Eq. 2) to evaluate the relationship between soil C fluxes and soil temperature, moisture and soil mineral N concentrations.

2 Materials and methods

2.1 Study sites

Four old-growth forests are referred to as Daxinganling boreal coniferous forest, Changbaishan temperate needle-broadleaved mixed forest, Dinghushan subtropical evergreen broad-leaved forest, and Xishuangbanna tropic monsoon rain forest from north to south, hereafter referred to as boreal, temperate, subtropical, and tropical forest, respectively (Fig. 1, Table 1). These forest sites expand from the mean annual temperature of −5.4°C in the boreal forest to 21.4°C in the tropical forest, and annual precipitation from 500 mm in cool temperate climate region to over 1600 mm in tropical and subtropical climate region. The total nitrogen deposition increases from 8.5 kg N ha^{-1} yr^{-1} in the boreal to 38.4 kg N ha^{-1} yr^{-1} in the subtropical. The boreal forest is a pure forest with Chinese larch (*Larix gmelinii*) as the predominant tree species (Jiang et al., 2002). The dominant vegetation species in the temperate forest are Korean pine (*Pinus koraiensis*), basswood (*Tilia amuresis*), Manchurian ash (*Fraxinus mandshurica*) and oak (*Quercus mortgolica*) in the tree layer (Zhang et al., 2006). The major species in the subtropical forest are guger-tree *(Schima superba)*, rose apple *(Syzygium jambos)*, henry chinkapin *(Castanopsis chinensis)* in tree layers (Mo et al., 2008). The most abundant species in the tropical forest are downy malugay (*Pometia tomentosa*), bayberry waxmyrtle-fruit (*Terminalia myriocarpa*), Yunan nutmeg (*Myristica yunnanensis*), South-Yunnan horsfieldia (*Horsfieldia tetratepala*), glabrous homalium (*Homalium laoticum*) (Werner et al., 2006). The soils are Greyzems, Luvisols, Ferralsols and Lixisols in the four old-growth forests from north to south, respectively (WRB, 2006). More extensive description on the sites was given in Table 1.

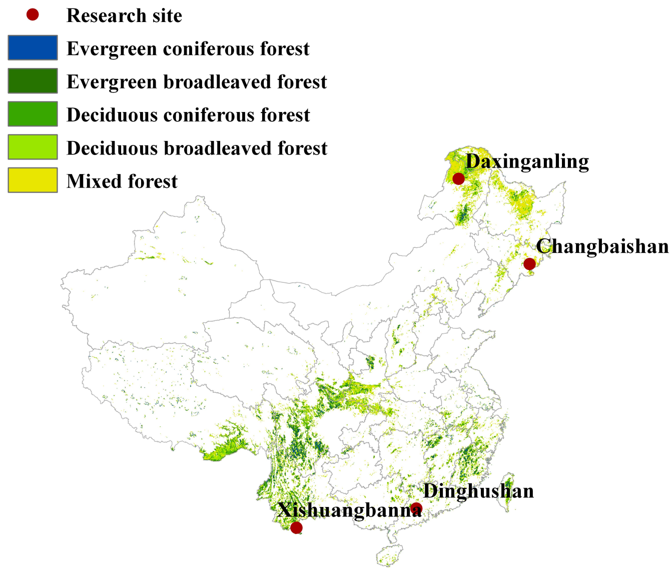

Fig. 1. Spatial distribution of soil CO_2 and CH_4 fluxes measurement sites in eastern China.

2.2 Soil CO_2 and CH_4 flux measurements

At each forest site, three replicate chambers were randomly designated to measure CO_2 and CH_4 fluxes applying static opaque chamber and gas chromatography method (Wang and Wang, 2003). The chambers were made of stainless-steel and consisted of a square collar (length × width × height = 50 cm × 50 cm × 10 cm) and a removable cover chamber (length × width × height = 50 cm × 50 cm × 50 cm). The collar was inserted directly into the forest floor about 10 cm below the floor surface, and the cover was placed on top during sampling and removed afterwards. The collars

Table 1. Stand characteristics and surface soil (0–20 cm) properties of the four old-growth forest sites.

Sites	Daxinganling[a]	Changbaishan[a]	Dinghushan[a,b]	Xishuangbanna[a,c]
Forest type	Boreal coniferous forest	Temperate mixed forest	Subtropical evergreen broadleaved forest	Tropic monsoon rain forest
Stand age (yr)	180	150	400	200
Location	50°56′ N, 121°30′ E	42°24′ N, 128°05′ E	23°10′ N, 112°34′ E	21°56′ N, 101°16′ E
Elevation (m)	810	740	300	720
Mean annual temperature (°C)	−5.4	2.8	20.9	21.4
Annual precipitation (mm)	500	750	1564	1557
N deposition (kg N ha^{-1} yr^{-1})	8.50	17.63	38.40	18.09
Biomass (Mg C ha^{-1})	56.1 (4.8)	67.2 (2.2)	87.7 (8.7)	73.5 (6.6)
Fine root biomass (Mg C ha^{-1})	2.40 (0.48)	2.82 (0.51)	4.90 (0.99)	3.06 (0.47)
Litter input (Mg C ha^{-1} yr^{-1})	2.50 (0.27)	4.52 (0.20)	8.42 (0.47)	11.56 (0.65)
Gravel (0.2–2 mm, %)	11.16	12.82	34.30	7.58
Sand (0.02–0.2 mm, %)	51.76	19.72	19.65	17.10
Silt (0.002–0.02 mm, %)	27.55	41.97	19.65	20.93
Clay (<0.002 mm, %)	9.53	25.49	26.22	54.39
SOC density (0–20 cm, kg m^{-2})	14.62 (0.35)	11.5 (0.46)	8.8 (0.58)	7.53 (0.17)
Total N (g kg^{-1})	1.83 (0.13)	1.18 (0.04)	2.50 (0.20)	1.45 (0.03)
C/N	25.14 (1.89)	21.84 (1.52)	12.8 (1.7)	11.33 (0.87)
Soil pH	6.03 (0.09)	5.85 (0.15)	3.80 (0.11)	4. 75 (0.22)

Data source:
[a] database of Chinese Ecosystem Research Network (CERN),
[b] Tang et al. (2006),
[c] Sha et al. (2005). Standard errors are in parentheses.

were installed on July 2001 at Changbaishan, August 2001 at Dinghushan, March 2002 at Xishuangbanna and September 2002 at Daxinganling, respectively. A fan with a diameter of 10 cm (4200 rpm ± 10%, 12V, 0.21 A) was installed on the top wall inside each chamber to make turbulence when chamber was closed. White insulating cover was added outside of the stainless steel cover to reduce the impact of direct radiative heating during sampling.

The soil C fluxes were measured between 9:00 and 11:00 a.m. (China Standard Time, CST) by fitting the chambers to the collars for 30 min. A diurnal study demonstrated that CO_2 and CH_4 fluxes measured from 9:00 to 11:00 were close to daily means (Tang et al., 2006). The four gas samples were taken by 100 mL plastic syringes at intervals of 0, 10, 20 and 30 min after closing the chambers. All gas samples were analyzed within 24 h following gas collection. Soil CO_2 and CH_4 fluxes were calculated based on their rate of concentration change within the chamber, which was estimated as the slope of linear regression between concentration and time (Wang and Wang, 2003). All the coefficients of determination (r^2) of the linear regression were more than 0.95 in our study. Positive and negative fluxes indicate forest soils function as net source and sink of CO_2 and CH_4, respectively.

Soil temperature and soil moisture at 10 cm below soil surface were monitored at each chamber simultaneously. Soil temperature was measured applying portable temperature probes (JM624 digital thermometer, Living-Jinming Ltd., China). Volumetric soil moisture (m^3 m^{-3}) was measured applying moisture probe meter (MPM160, Meridian Measurement, China). Field measurements were carried out weekly in the vegetative season (from May to October) and monthly in the non-vegetative season (from November to April next year).

2.3 Soil sampling and mineral N analysis

In the middle ten days of each month during the vegetative season, mineral soils nearby the gas chambers were taken from 0–10 cm depth applying an auger (5 cm in diameter) after careful removal of O-horizon. Soil sampling was conducted in the same way in the non-vegetative season at the tropical and subtropical forest sites. However, soil samples were not collected in the non-vegetative season because frozen soil occurred from November to April next year at the boreal and temperate forest sites. Four samples were collected at each site. Soils were immediately passed through a 2 mm sieve to remove roots, gravel and stones. Soil samples were extracted in 100 ml 0.2 M KCl solution and shaken for 1 h. The soil suspension was subsequently filtered through Whatman No. 40 filter papers for NH_4^+-N and NO_3^--N determination on a continuous-flow autoanalyzer (Bran Luebbe, Germany).

2.4 Non-linear relationship between C fluxes and soil temperature

An exponential growth model was used to fit the relationship between soil CO_2 flux and soil temperature. The sensitivity of soil CO_2 flux to soil temperature at 10 cm depth (Q_{10}) was obtained from a coefficient, B, in the exponential equation (Eq. 1, 2) (Lloyd and Taylor, 1994):

$$F_{CO_2} = F_0 e^{BT} \tag{1}$$

$$Q_{10} = F_{T+10}/F_T = e^{10B} \tag{2}$$

where, F_{CO_2} is the soil CO_2 flux, T is the soil temperature, F_0 is the soil CO_2 flux as soil temperature equal to zero degree Celcius, and B is a regression coefficient.

A Gaussian equation (Eq. 3) was used to fit the relationship between soil CH_4 flux and soil temperature:

$$F_{CH_4} = a e^{\left[-0.5\left(\frac{T-T_0}{b}\right)^2\right]} \tag{3}$$

where, a and b are the parameters of the Gausian equation, and T_0 is the optimal soil temperature as soil CH_4 oxidation is the maximum.

2.5 Statistical analysis

A repeated measures analyses of variance (ANOVA) was performed on monthly mean to test the variation of soil temperature, moisture, mineral N contents and soil C fluxes in forests and seasons. Additionally, the relationships between CO_2 and CH_4 fluxes and soil variables (temperature, moisture and mineral N) were examined in a way of linear or nonlinear regression models fitting. Mean Square Error (MSE) and R^2 of the model parameters were used to determine goodness-of-fit. All statistical analyses were performed using SAS software (SAS Institute, 2001). A p-value$<$0.05 was used to reject the null hypothesis that the model is not significant.

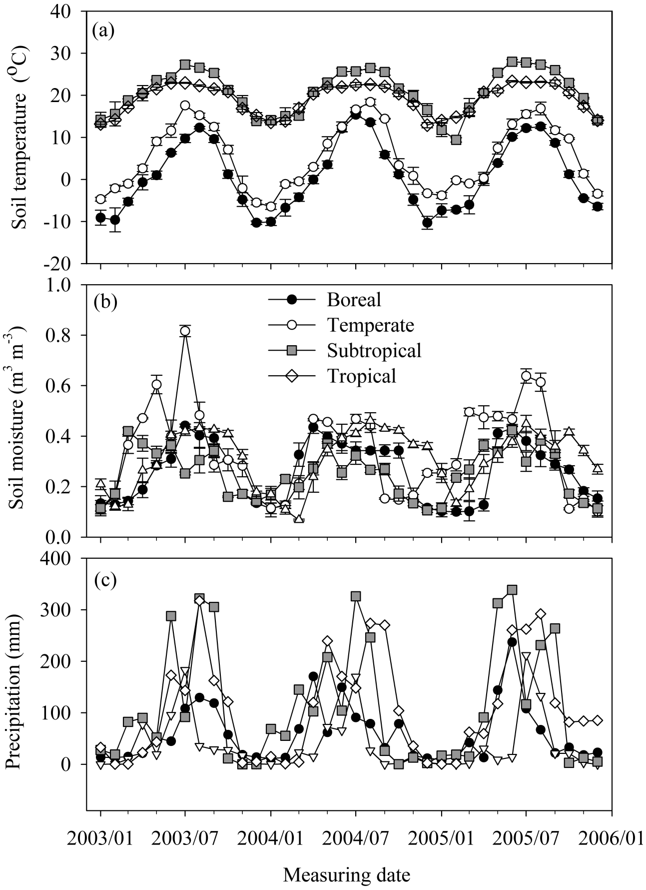

Fig. 2. The seasonal variation of soil temperature and moisture (± 1 SE) at a depth of 10 cm and average precipitation in the four forests from 2003 to 2005.

3 Results

3.1 Seasonality of primary environmental variables

Soil temperature and moisture presented clear seasonal courses (Fig. 2a), being highest in summer and lowest in winter. Soil moisture was correlated strongly with soil temperature at all the forest sites, except in the subtropical forest (Fig. 2a and Fig. 2b). Monthly average precipitation showed similar pattern to soil moisture in the four old-growth forests (Fig. 2c). In both vegetative and non-vegetative seasons, there was significant difference of soil temperature and moisture among the four old-growth forests, but no trend in soil moisture from north to south (Table 2).

3.2 Seasonality of soil mineral N

In the boreal, temperate and tropical forests, the two peaks of NH_4^+-N concentration occurred in the early vegetative season between April and May and in summer between July and August (Fig. 3a). However, the NH_4^+-N concentration remained relatively constant in the subtropical forest in the whole year

Table 2. Effects of forest type and season on the mean (standard error) of soil temperature, moisture, mineral N concentrations and soil-atmospheric C exchanges*.

Forest	Soil temperature (°C)		Soil moisture (m^3 m^{-3})		NH_4^+-N content (mg kg^{-1})		NO_3^--N content (mg kg^{-1})		Soil CO_2 flux (Mg CO_2 ha^{-1} $season^{-1}$)		Soil CH_4 flux (kg CH_4 ha^{-1} $season^{-1}$)	
sites	non-veg.	veg.	non-veg.	veg.	non-veg.	veg.	non-veg.	veg.	non-veg.	veg.	non-veg.	veg.
Boreal	−5.75 (0.75) c	8.15 (1.10) d	0.17 (0.02) b	0.37 (0.01) ab	–	12.78 (0.80)b	–	2.01 (0.19) c	2.31 (0.03) b	15.78 (0.21) a	0.78 (0.13) a	−0.82 (0.03) ab
Temperate	−1.71 (0.61) b	12.29 (0.98) c	0.26 (0.03) a	0.42 (0.04) a	–	9.25 (0.66)c	–	4.57 (0.29) bc	3.28 (0.29) b	16.80 (0.94) a	−1.18 (0.96) ab	−1.11 (0.79) ab
Sub tropical	16.38 (0.77) a	25.20 (0.48) a	0.21 (0.02)ab	0.30 (0.02) b	1.79 (0.10)	2.75 (0.13)d	5.21 (0.68)	16.15 (2.09) a	12.21 (1.20) a	23.19 (1.58) a	−2.79 (0.47) b	−2.36 (0.49) b
Tropical	16.09 (0.60) a	22.11 (0.22) b	0.22 (0.02)ab	0.40 (0.01) a	18.75 (1.10)	22.63 (0.43) a	5.86 (0.26)	7.46 (0.10) b	12.86 (1.93) a	21.68 (3.08) a	−3.66 (0.59) b	1.18 (1.64) a

* Vegetative season is from May to October and non-vegetative season is from November to April next year. Negative CH_4 values are CH_4 uptake. Means followed by different letters in the same column are significantly different (Turky's HSD comparison).

(Fig. 3a). In the vegetative season, there was a significant difference in NH_4^+-N concentration among forests (p <0.001), with the averages (from 2003 to 2005) being 12.78 ± 0.52, 9.25 ± 0.66, 2.75 ± 0.13 and 22.63 ± 0.43 mg N kg^{-1} in the boreal, temperate, subtropical and tropical forests, respectively (Table 2).

In contrast, only the subtropical forest soil showed strong seasonal variation in NO_3^--N concentration, with peaks of soil NO_3^--N occurring between June and August (Fig. 3b). However, in the boreal and temperate forests NO_3^--N concentration tended to decrease in early spring and then slightly rose in the late vegetative season (Fig. 3b). From 2003 to 2005, mean NO_3^--N concentrations in the vegetative season were significantly different among four old-growth forests. Their order was as follows: subtropical forest (16.15 ± 2.09 mg N kg^{-1}) > tropical forest (7.46 ± 0.10) > temperate forest (4.57 ± 0.29) > boreal forest (2.01 ± 0.19) (p <0.001) (Table 2).

3.3 Seasonality of soil CO_2 and CH_4 fluxes

Soil CO_2 flux showed a consistent variation with soil temperature. The seasonal difference in CO_2 flux was more pronounced in the boreal and temperate forests than in the tropical and subtropical forests (Fig. 4a). Although total soil CO_2 flux increased ranging from 15.78 to 23.19 Mg CO_2 ha^{-1} $season^{-1}$ in the vegetative season, the difference among four forests was not significant (p >0.05, Table 2). In the non-vegetative season, total CO_2 flux in the boreal and temperature forests ranged from 2.31 to 3.28 M CO_2, ha^{-1} season $^{-1}$, which were significantly lower than those in the tropical and subtropical forests ranging from 12.21 to 12.86 Mg CO_2 ha^{-1} $season^{-1}$ (p <0.001, Table 2).

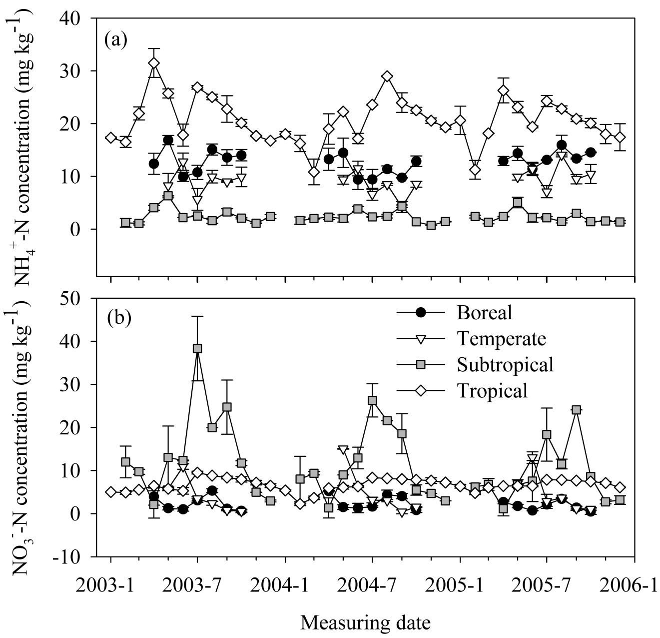

Fig. 3. The seasonal variation of soil NH_4^+-N and NO_3^--N concentrations (± 1 SE) at a depth of 10 cm in the four forests from 2003 to 2005.

Soil CH_4 flux also showed seasonal variations. The higher uptake and emission in the boreal and temperate forests were observed in summer and in winter, respectively (Fig. 4b). The subtropical forest soil behaved as a net soil CH_4 sink throughout the study period (Fig. 4b). There was a significant difference in CH_4 flux among four old-growth forests in both vegetative and non-vegetative seasons (Table 2). In the non-vegetative season, the boreal forest behaved as a CH_4 source (0.78 kg CH_4 ha^{-1} $season^{-1}$) and

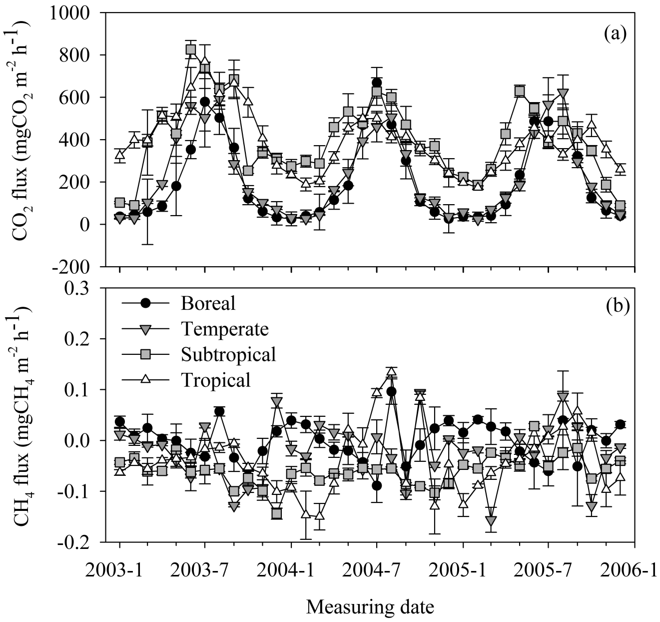

Fig. 4. Seasonal patterns of CO_2 and CH_4 fluxes (± 1 SE) measured in the four forests.

other forests behaved as CH_4 sinks ranging from -1.18 to $-3.66\,\mathrm{kg\,CH_4\,ha^{-1}\,season^{-1}}$ (Table 2). However, in the vegetative season, only the tropical monsoon rain forest soil was a source of CH_4 of $1.18\,\mathrm{kg\,CH_4\,ha^{-1}\,season^{-1}}$, whereas the soil CH_4 sink occurred in other forests ranging from -0.82 to $-2.36\,\mathrm{kg\,CH_4\,ha^{-1}\,season^{-1}}$ (Fig. 4b and Table 2).

3.4 Relationships between soil temperature, moisture and C fluxes

Soil CO_2 flux was fitted with soil temperature in the equation (Eq. 1), and the results indicated that soil temperature could explain 49%–96% of CO_2 flux variation (Fig. 5a and Table 3). The average Q_{10} was significantly higher in the boreal (3.08) and temperate forests (2.61) than in the tropical (2.16) and subtropical forests (2.05) (Table 3). Soil CO_2 flux and soil moisture had a positive linear relationship, explaining 40%–49% of variation in CO_2 flux (Fig. 5b and Table 3). These results showed that soil CO_2 flux was mainly driven by soil temperature, and followed by soil moisture.

For all forests, soil CH_4 flux was negatively correlated with soil temperature when soil temperature is less than the optimal value, while a positive relationship appeared when soil temperature is above the temperature (Fig. 5c). This optimal value increased with a decrease in latitude. For instance, the values were 7.3°C and 7.8°C in the boreal and temperate forests, 15.7°C and 18.0°C in the tropical and subtropical forests, respectively (Table 3). If forest types were not considered and all observed data were included in the model, the relationship between CH_4 flux and soil temperature was fitted well with equation (Eq. 3) and the average optimal soil temperature was 15°C (Fig. 5c and Table 3). A negative relationship between CH_4 flux and soil moisture in the boreal forest, and a positive relationship between them in the tropical and subtropical forests were observed, explaining 19%–42% of variation in CH_4 fluxes (Fig. 5d and Table 3). These results suggested that the response of soil CH_4 flux to soil temperature depended upon the optimal soil temperature and the response to soil moisture varied by forest type.

3.5 Relationship between soil mineral N and soil C fluxes

Soil CO_2 fluxes in the tropical and subtropical forests were positively correlated to the concentrations of NH_4^+-N and NO_3^--N in the 10 cm soil (Fig. 6a, b and Table 4). However, the relationships between soil CO_2 fluxes and mineral N concentrations were not statistically significant in the boreal and temperate forests (Fig. 6a, b). Additionally, a positive correlation between soil CH_4 flux and soil NH_4^+-N was observed in the tropical forest (Fig. 6c and Table 4). In the boreal and tropical forests where CH_4 emission occurred periodically, soil CH_4 flux was positively correlated to NO_3^--N concentration (Fig. 6d and Table 4). Taking four forests together, soil CO_2 flux was positively related to soil NO_3^--N concentration and soil CH_4 flux was positively related to NH_4^+-N concentration (Fig. 6b, d and Table 4). These results suggested that the accumulation of soil NO_3^--N and NH_4^+-N were consistent with the increase of gas emission of CO_2 and CH_4 in the old-growth forests in eastern China, respectively.

4 Discussion

4.1 Comparisons with other studies

The annual mean soil CO_2 fluxes of 18.09 ± 0.22 and $20.08 \pm 1.20\,\mathrm{Mg\,CO_2\,ha^{-1}\,yr^{-1}}$, respectively in the boreal and temperate forests (mean $\pm$ se) fall in the range of 11.59 to $40.15\,\mathrm{Mg\,CO_2\,ha^{-1}\,yr^{-1}}$ reported by a number of worldwide studies (e.g. Borken and Brumme, 1997; Maljanen et al., 2001; Merino et al., 2004; Falk et al., 2005; Sulzman et al., 2005; Zerva and Mencuccini, 2005). However, the annual mean soil CO_2 flux of 35.40 ± 2.42 and $34.54 \pm 4.99\,\mathrm{Mg\,CO_2\,ha^{-1}\,yr^{-1}}$, respectively in the subtropical and tropical forests are higher than the reported average in an evergreen tropical forest on the island of Hawaii ($26.34\,\mathrm{Mg\,CO_2\,ha^{-1}\,yr^{-1}}$, Townsend et al., 1995) and in a tropical monsoon forest in Tainland ($25.6\,\mathrm{Mg\,CO_2\,ha^{-1}\,yr^{-1}}$, Hashimoto et al., 2004), but lower than that in a subtropical moist forest, Queensland, Australia ($51.07\,\mathrm{Mg\,CO_2\,ha^{-1}\,yr^{-1}}$, Butterbach-Bahl et al., 2004) and tropical forests in South America (36.94–$52.68\,\mathrm{Mg\,CO_2\,ha^{-1}\,yr^{-1}}$, Garcia-Montiel et al., 2004; Sotta et al., 2007).

Table 3. Parameter values of the models for the relationship between the soil CO_2 and CH_4 fluxes and soil temperature (T) at a depth of 10 cm and moisture (M) at the top 10 cm soil layer.

Forest	a	b	T_0*	p	R^2	MSE	Q_{10}
(a) $F_{CO_2} = a^* \exp(b^* T)$							
Boreal	124.17	0.11		< 0.0001	0.96	41.13	3.08
Temperate	106.11	0.10		< 0.0001	0.85	75.81	2.61
Subtropical	85.41	0.07		0.001	0.61	116.42	2.05
Tropical	87.53	0.08		0.003	0.49	103.97	2.16
All forests	147.09	0.05		< 0.0001	0.65	120.07	1.70
(b) $F_{CO_2} = a + b^* M$							
Boreal	−91.28	1109.94		< 0.0001	0.45	157.59	
Temperate	−29.62	756.19		< 0.0001	0.49	140.35	
Subtropical	67.63	1329.06		< 0.0001	0.49	132.60	
Tropical	146.44	796.41		< 0.0001	0.40	113.69	
All forests	72.03	806.68		< 0.0001	0.29	172.03	
(c) $F_{CH_4} = a * \exp(-0.5^*((T - T_0)/b)^2)$							
Boreal	−0.05	2.53	7.3	0.04	0.17	0.04	
Temperate	−0.04	4.19	7.8	0.004	0.31	0.03	
Subtropical	−0.07	9.25	18.0	0.004	0.82	0.03	
Tropical	−0.11	2.70	15.7	0.0003	0.61	0.05	
All forests	−0.05	8.25	15.3	< 0.0001	0.37	0.05	
(d) $F_{CH_4} = a + b^* M$							
Boreal	0.04	−0.16		0.002	0.25	0.04	
Subtropical	−0.09	0.14		0.008	0.19	0.03	
Tropical	−0.17	0.38		< 0.0001	0.42	0.06	
All forests	−0.05	0.07		0.0134	0.28	0.05	

* T_0 is the optimal soil temperature at which soil CH_4 oxidation rates reach the maximum values.

Table 4. Model parameters and coefficients for the relationship between the soil CO_2 and CH_4 fluxes and soil mineral N concentrations at the top 10 cm soil layer.

Forest	a	b	p	R^2	MSE
(a) $F_{CO_2} = a + b^* NH_4^+$					
Subtropical	295.71	54.40	0.03	0.14	169.14
Tropical	39.26	17.13	0.001	0.27	124.81
(b) $F_{CO_2} = a + b^* NO_3^-$					
Subtropical	291.62	11.61	0.0007	0.31	151.12
Tropical	30.73	54.63	0.0004	0.32	120.85
All forests	307.44	11.44	< 0.0001	0.17	152.96
(c) $F_{CH_4} = a + b^* NH_4^+$					
Tropical	−0.23	0.010	0.001	0.28	0.071
All forests	−0.064	0.003	0.0006	0.11	0.059
(d) $F_{CH_4} = a + b^* NO_3^-$					
Boreal	−0.048	0.014	0.02	0.24	0.039
Tropical	−0.238	0.032	0.0003	0.32	0.069

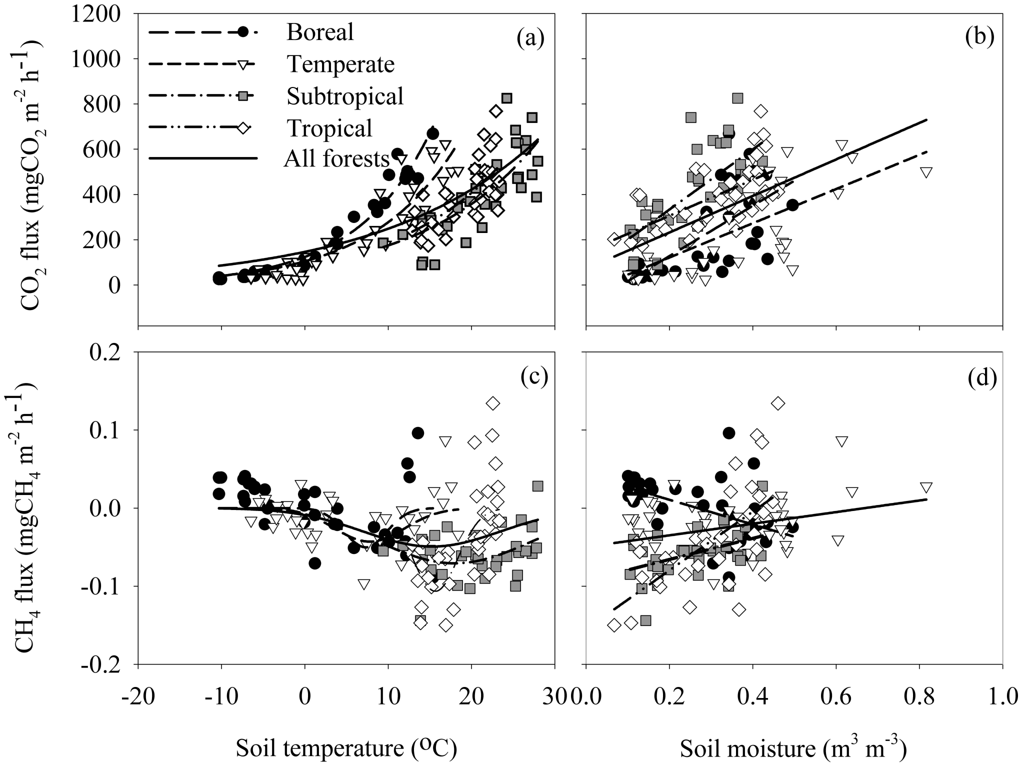

Fig. 5. Relationships of CO_2 and CH_4 fluxes to soil temperature and moisture at a depth of 10 cm in the four forests.

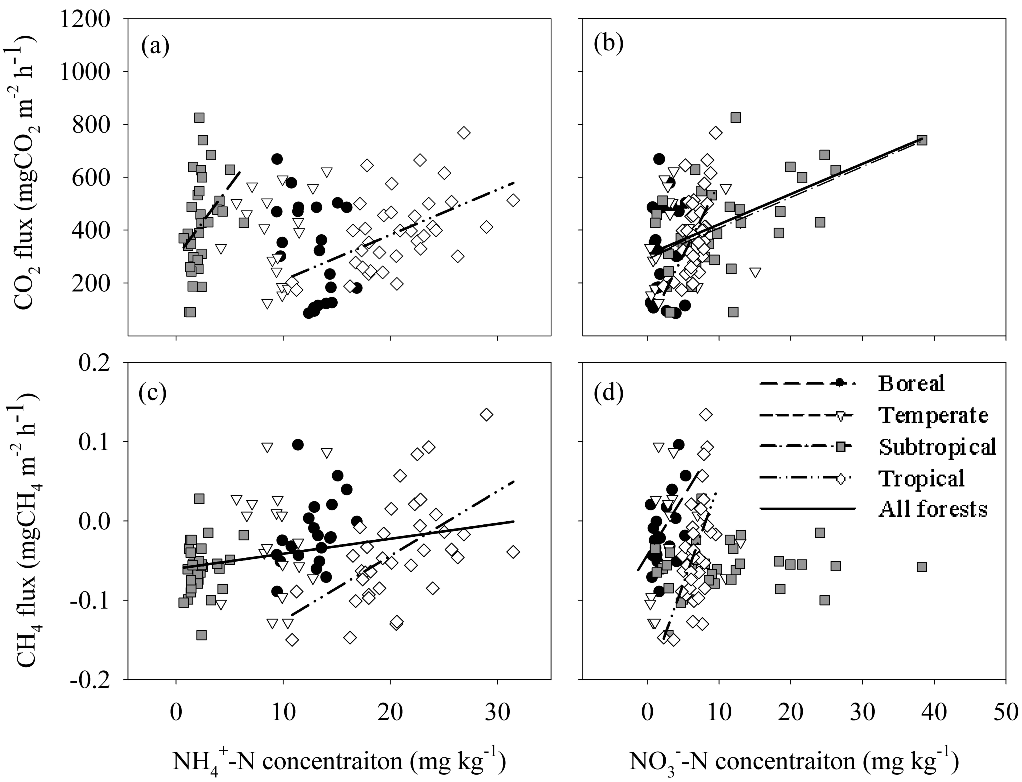

Fig. 6. Relationships of CO_2 and CH_4 fluxes to soil NH_4^+-N and NO_3^--N concentrations at a depth of 10 cm in the four forests.

The old-growth forest soils in eastern China represented efficient CH_4 sinks with the annual mean of -0.04 ± 0.11 kg CH_4 ha^{-1} yr^{-1} (boreal), -2.29 ± 0.70 kg CH_4 ha^{-1} yr^{-1} (temperate), -2.48 ± 1.07 kg CH_4 ha^{-1} yr^{-1} (tropical) and -5.15 ± 0.96 kg CH_4 ha^{-1} yr^{-1} (subtropical). The boreal forest soil took up CH_4 in the vegetative season (-0.82 ± 0.03 kg CH_4 ha^{-1}), but emitted CH_4 when soils were frozen in the non-vegetative season (0.78 ± 0.13 kg CH_4 ha^{-1}). This result was the same as those (-1.04–4.95 kg CH_4 ha^{-1} yr^{-1}) found in typical boreal forest soils in Alaska and Canada (Simpson et al., 1997; Billings et al., 2000; Kim et al., 2007). Conversely, for the atmospheric CH_4 the tropical forest soil behaved as a sink in the vegetative season and as a source in the non-vegetative season, respectively. Our data in the temperate forest were in the same range ($-2.00\sim-7.28$ kg CH_4 ha^{-1} yr^{-1}) as found in Asia, Europe and USA (Teepe et al., 2004; Suwanwaree and Robertson, 2005; Jang et al., 2006; Morishita et al., 2007), and were less than the global average of -5.60 kg CH_4 ha^{-1} yr^{-1} (Jang et al., 2006). Additionally, CH_4 fluxes in the tropical and subtropical forest soils were comparable with those of other tropical forest soils ($-2.10\sim-6.59$ kg CH_4 ha^{-1} yr^{-1}, Verchot et al., 2000; Davidson et al., 2000; Silver et al., 2005; Ishizuka et al., 2005; Werner et al., 2006, Werner et al., 2007).

4.2 Effects of soil temperature and moisture on soil C fluxes

With an increase in soil temperature, soil CO_2 flux increased, whereas the temperature sensitivity (Q_{10}) tended to decrease at warmer sites. In the boreal and temperate forests, soil warming can enhance the soil microbial activities and root growth sharply during the short summer (Zheng et al., 2009). This leads to an active decomposition of soil organic C and the enhancement of plant-derived CO_2 release from root respiration. However, the temperature limitation on root growth and soil microbial activities is low in tropical and subtropical forest ecosystems (Zheng et al., 2009). Besides, the labile pool of soil organic carbon (SOC) is an important substrate for soil respiration, and the composition of microbial community are linked to quantity/ quality of SOC (Gu et al., 2004; Knorr et al., 2005b; Fierer et al., 2005; Zheng et al., 2009). When other environmental factors are fixed, soil CO_2 flux tends to be higher under the conditions of higher SOC content. Gradient variation in SOC storage in the four old-growth forests also supported the above explanation (Table 1), which suggested that the acclimation of soil CO_2 flux to warming could be also induced by the lower temperature sensitivity with lower SOC content in the subtropical and tropical forests (Melillo et al., 2002).

Both soil CO_2 flux and Q_{10} value are closely related to soil moisture. Xu and Qi (2001) and Rey et al. (2002) found that soil CO_2 flux increased with increasing soil moisture when soil water-filled pore space (WFPS) was below 60%. In our study, soil moisture contents across four forest sites were generally less than 0.5 m^3 m^{-3} in the whole year (Fig. 5b, d), which were equivalent to 55% of WFPS calculated from the equation described by Franzluebbers (1999). Additionally, the Q_{10} value of forest ecosystems tended to decrease with mean annual precipitation (Table 1 and 3), which was consistent with a recent study (Peng et al., 2009). Wang et al. (2006) also suggested that the Q_{10} tended to increase with soil moisture until reaching a threshold (0.45 g H_2O g^{-1} soil), and then decline, which was mainly attributed to limitation of oxygen diffusion.

CH_4 oxidation in soil is controlled by CH_4 and O_2 availability in water-unsaturated forest soil (Teh et al., 2005). When the diffusion rates of CH_4 and O_2 from the atmosphere into the soil are equal to soil CH_4 and O_2 consumption, soil CH_4 oxidation rates reach the maximum values at a given temperature. Cai and Yan (1999) called this temperature as the optimal temperature. The optimal temperature for soil CH_4 oxidation varies with bioclimatic areas, about 20–30°C in low latitude region (Boeckx and VanCleemput, 1996; Cai and Yan, 1999), 5–25°C in middle latitude region (Castro et al., 1995), and less than 10°C in high latitude region (van den Pol-van Dasselaar et al., 1998). Our results fall in the same ranges described above. When soil temperature is relatively low, the CH_4 and O_2 diffusion potentials from the atmosphere to soil are higher than soil CH_4 and O_2 consumption rates due to weak soil microbial activity (Nedwell and Watson, 1995). In this case, soil temperature is the limiting factor for CH_4 oxidation (Peterjohn et al., 1994; Prieme and Christensen, 1997). However, if soil temperature continually rises to superior the optimal level, the reproduction and activity of methanotrophs in soils will gradually decrease because methanotrophs fail to compete with nitrifiers and other microbes for the limited oxygen in soil air (Horz et al., 2005; Castaldi and Fierro, 2005; Borken et al., 2006).

4.3 Effects of soil mineral N on soil CO_2 flux

The positive correlation between soil CO_2 flux and soil NO_3^--N concentration across four forests suggested that NO_3^--N accumulation caused by environmental change could promote forest soil CO_2 emission. The ability of plants to compete available N (especially NO_3^--N) is often stronger than soil microorganisms in N-limiting natural forest ecosystems (Jaeger et al., 1999). Soil NO_3^--N accumulation in forest ecosystems tended to increase fine root/ biomass ratio, which was a good index of C allocation to root. Our calculated data showed that the fine root/biomass ratio (0.06) in the subtropical forest with higher soil NO_3^--N content was significantly higher than those (0.04) in other forest ecosystems (Table 1). This could partially contribute to the higher autotrophic respiration. However, excessive NO_3^- accumulation and occurrence of ecosystem N saturation would decrease fine root biomass and soil respiration (Mo et al., 2008; Fang et al., 2009).

Soil NO_3^--N accumulation could also increase litter decomposition rate due to the decline of its C/N ratio with more mineral N incorporated in organic matter (Berg et al., 1998; Hobbie and Gough, 2004). In addition, soil CO_2 fluxes were positively correlated to both NO_3^--N and NH_4^+-N in N-rich tropical and subtropical forests (Fig. 6a, b). This could be partially attributed to microbial immobilization of soil available N. Soil microorganism need more available C to immobilize redundant mineral N in N-rich forests, and this would stimulate soil microbial activity, elevate organic matter decomposition and increase heterotrophic respiration (McDowell et al., 2004). All these are consistent with experimental findings that N addition promoting soil respiration in N-limited forest ecosystems (Micks et al., 2004; McDowell et al., 2004). Based on meta analysis, Knorr et al. (2005a) also observed that litter decomposition was stimulated by N addition at field sites exposed to low ambient N deposition ($<5\,\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$). But litter decomposition would be inhibited by N additions when fertilization rates were 2–20 times larger than the anthropogenic N-deposition level, when ambient N deposition was 5–10 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ (Knorr et al., 2005a).

4.4 Effects of soil mineral N on soil CH_4 flux

The positive relationship between soil NH_4^+-N and soil CH_4 flux across four forests (Fig. 6c) suggested that soil NH_4^+-N accumulation can significantly inhibit CH_4 oxidation. This result is consistent with findings in many N addition experiments that adding N decreased CH_4 uptake by 14% to 51% relative to the control (e.g. King and Schnell, 1994; Sitaula et al., 1995; Gulledge et al., 2004; Zhang et al., 2008). High concentration of soil NH_4^+-N could significantly inhibit methanotrophic activities in soils because it stimulates the quantity of NH_4^+-oxidizer bacteria in the organic layers of forest soil (King and Schnell, 1994; Whalen and Reeburgh, 2000). This is also an acceptable explanation for the highest soil CH_4 uptake in the subtropical forest. Due to the relative high N deposition rate (more than 30 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$) and the high initial content of soil N, the subtropical forest at Dinghushan site, where soil mineral N is dominated by soil NO_3^--N (Fig. 3) and soil N leaching and gaseous emission is very high (Zhang et al., 2008; Fang et al., 2009), has already reached N saturation (Mo et al., 2008). However, the tropical forest at Xishuangbanna site where economy is undeveloped and N deposition is low, soil mineral N is still dominated by soil NH_4^+-N and is not unsaturated yet (Fig. 3). On the contrary, because soil NH_4^+ in the boreal and temperate forests was mainly assimilated by plants or immobilized by soil clay mineral, the relatively lower CH_4 uptake was attributed to other reasons such as lower substrate availability or lower gas diffusion rather than NH_4^+ inhibition. For example, low temperature and frozen layer in winter as well as the thicker O-horizon obstruct the diffusion of CH_4 into soil, which will indirectly decrease the uptake of soil CH_4 (Elberling et al., 2008).

The positive relationships between soil NO_3^--N and soil CH_4 flux in the tropical and boreal forests (Fig. 6d) were inconsistent with other studies that NO_3^- has either increase or no effect on CH_4 uptake (Dunfield et al., 1995; Corton et al., 2000). In general, soil nitrification consumes soil NH_4^+-N and subsequently accumulates soil NO_3^- in warm and mesic condition. Unsaturated soil and no NH_4^+-N accumulation favor soil CH_4 uptake in subtropical and temperate forests. However, no significant accumulation of soil NO_3^--N within the study period in the boreal and tropical forests partially attributed to soil denitrification, especially during soil freezing in the boreal forest in winter and soil water-logging of the tropical forest in rain season. Hydroxylamine (NH_2OH) or nitrite (NO_2^-) produced via NH_4^+ oxidation and NO_3^- reduction could produce a toxic inhibition on CH_4 uptake (King and Schnell, 1994).

5 Conclusions

Soil CO_2 emissions of old-growth forests in eastern China were mainly driven by temperature, followed by soil moisture, NO_3^--N content. The apparent sensitivity of CO_2 flux to soil temperature (Q_{10}) tended to decrease with the increase in air temperature and moisture, indicating the acclimation of soil CO_2 flux to warming in forests with lower SOC content. Soil NO_3^- accumulation caused by warming and nitrogen deposition was often accompanied by an increase in soil CO_2 emission, which could be partially attributed to the increase of C allocation to root and decomposability of organic materials.

Soil CH_4 uptake decreased with the increase in soil moisture. The response of soil CH_4 flux to temperature was dependent upon the optimal value of soil temperature in each forest. Soil NH_4^+-N consumption tended to promote soil CH_4 uptake in the old-growth forests, whereas soil NO_3^- accumulation was not conducive to CH_4 oxidation in anaerobic condition. The mechanism by which soil mineral N affected CH_4 uptake included both a competitive inhibition of monooxygenase by NH_4^+ and a toxic inhibition by hydroxylamine or nitrite. These results indicate that soil mineral N dynamics largely affects the soil gas fluxes of CO_2 and CH_4 in the old-growth forests, along with climate conditions.

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References

Berg, M. P., Kniese, J. P., Zoomer, R., and Verhoef, H. A.: Long-term decomposition of successive organic strata in a nitrogen saturated Scots pine forest soil, Forest Ecol. Manag., 107, 159–172, 1998.

Bergner, B., Johnstone, J., and Treseder, K. K.: Experimental warming and burn severity alter soil CO_2 flux and soil functional groups in a recently burned boreal forest, Glob. Change Biol., 10, 1996–2004, 2004.

Billings, S. A., Richter, D. D., and Yarie, J.: Sensitivity of soil methane fluxes to reduced precipitation in boreal forest soils, Soil Biol. Biochem., 32, 1431–1441, 2000.

Boeckx, P. and VanCleemput, O.: Methane oxidation in a neutral landfill cover soil: Influence of moisture content, temperature, and nitrogen-turnover, J. Environ. Qual., 25, 178–183, 1996.

Borken, W. and Brumme, R.: Liming practice in temperate forest ecosystems and the effects on CO_2, N_2O and CH_4 fluxes, Soil Use Manage., 13, 251–257, 1997.

Borken, W., Davidson, E. A., Savage, K., Sundquist, E. T., and Steudler, P.: Effect of summer throughfall exclusion, summer drought, and winter snow cover on methane fluxes in a temperate forest soil, Soil Biol. Biochem., 38, 1388–1395, 2006.

Bowden, R. D., Davidson, E., Savage, K., Arabia, C., and Steudler, P.: Chronic nitrogen additions reduce total soil respiration and microbial respiration in temperate forest soils at the Harvard Forest, Forest Ecol. Manag., 196, 43–56, 2004.

Butterbach-Bahl, K., Kock, M., Willibald, G., Hewett, B., Buhagiar, S., Papen, H., and Kiese, R.: Temporal variations of fluxes of NO, NO_2, N_2O, CO_2, and CH_4 in a tropical rain forest ecosystem, Global Biogeochem. Cy., 18, GB3012, doi:10.1029/2004gb002243, 2004.

Cai, Z. C. and Yan, X. Y.: Kinetic model for methane oxidation by paddy soil as affected by temperature, moisture and N addition, Soil Biol. Biochem., 31, 715–725, 1999.

Castaldi, S. and Fierro, A.: Soil-atmosphere methane exchange in undisturbed and burned Mediterranean shrubland of southern Italy, Ecosystems, 8, 182–190, 2005.

Castro, M. S., Steudler, P. A., Melillo, J. M., Aber, J. D., and Bowden, R. D.: Factors controlling atmospheric methane consumption by temperate forest soils, Global Biogeochem. Cy., 9, 1–10, 1995.

Chantigny, M. H., Angers, D. A., Prevost, D., Simard, R. R., and Chalifour, F. P.: Dynamics of soluble organic C and C mineralization in cultivated soils with varying N fertilization, Soil Biol. Biochem., 31, 543–550, 1999.

Corre, M. D., Brumme, R., Veldkamp, E., and Beese, F. O.: Changes in nitrogen cycling and retention processes in soils under spruce forests along a nitrogen enrichment gradient in Germany, Glob. Change Biol., 13, 1509–1527, 2007.

Corton, T. M., Bajita, J. B., Grospe, F. S., Pamplona, R. R., Assis, C. A., Wassmann, R., Lantin, R. S., and Buendia, L. V.: Methane emission from irrigated and intensively managed rice fields in Central Luzon (Philippines), Nutr. Cycl. Agroecosys., 58, 37–53, 2000.

Dalal, R. C. and Allen, D. E.: Greenhouse gas fluxes from natural ecosystems, Aust. J. Bot., 56, 369–407, 2008.

Davidson, E. A., Ishida, F. Y., and Nepstad, D. C.: Effects of an experimental drought on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest, Glob. Change Biol., 10, 718–730, 2004.

Davidson, E. A., Keller, M., Erickson, H. E., Verchot, L. V., and Veldkamp, E.: Testing a conceptual model of soil emissions of nitrous and nitric oxides, Bioscience, 50, 667–680, 2000.

Dunfield, P. F., Topp, E., Archambault, C., and Knowles, R.: Effect of nitrogen fertilizers and moisture content on CH_4 and N_2O Fluxes in a Humisol: Measurements in the field and intact soil cores, Biogeochemistry, 29, 199–222, 1995.

Elberling, B., Nordstrom, C., Grondahl, L., Sogaard, H., Friborg, T., Christensen, T. R., Strom, L., Marchand, F., and Nijs, I.: High-arctic soil CO_2 and CH_4 production controlled by temperature, water, freezing and snow, Adv. Ecol. Res., 40, 441–472, 2008.

Falk, M., Paw U, K. T. P., Wharton, S., and Schroeder, M.: Is soil respiration a major contributor to the carbon budget within a Pacific Northwest old-growth forest?, Agr. Forest Meteorol., 135, 269–283, 2005.

Fang, Y. T., Zhu, W. X., Gundersen, P., Mo, J. M., Zhou, G. Y., and Yoh, M.: Large loss of dissolved organic nitrogen from nitrogen-saturated forests in subtropical China, Ecosystems, 12, 33–45, 2009.

Fierer, N., Craine, J., McLauchlan, K., and Schimel, J.: Litter quality and the temperature sensitivity of decomposition, Ecology, 86, 320–326, 2005.

Franzluebbers, A. J.: Microbial activity in response to water-filled pore space of variably eroded southern Piedmont soils, Appl. Soil Ecol., 11, 91–101, 1999.

Garcia-Montiel, D. C., Melillo, J. M., Steudler, P. A., Tian, H., Neill, C., Kicklighter, D. W., Feigl, B., Piccolo, M., and Cerri, C. C.: Emissions of N_2O and CO_2 from terra firme forests in Rondonia, Brazil, Ecol. Appl., 14, S214–S220, 2004.

Gu, L. H., Post, W. M., and King, A. W.: Fast labile carbon turnover obscures sensitivity of heterotrophic respiration from soil to temperature: A model analysis, Global Biogeochem. Cy., 18, GB1022, doi:10.1029/2003gb002119, 2004.

Gulledge, J., Hrywna, Y., Cavanaugh, C., and Steudler, P. A.: Effects of long-term nitrogen fertilization on the uptake kinetics of atmospheric methane in temperate forest soils, Fems Microbiol. Ecol., 49, 389–400, 2004.

Hashimoto, S., Tanaka, N., Suzuki, M., Inoue, A., Takizawa, H., Kosaka, I., Tanaka, K., Tantasirin, C., and Tangtham, N.: Soil respiration and soil CO_2 concentration in a tropical forest, Thailand, J. For. Res.-Jpn., 9, 75–79, 2004.

Hobbie, S. E. and Gough, L.: Litter decomposition in moist acidic and non-acidic tundra with different glacial histories, Oecologia, 140, 113–124, 2004.

Horz, H. P., Rich, V., Avrahami, S., and Bohannan, B. J. M.: Methane-oxidizing bacteria in a California upland grassland soil: Diversity and response to simulated global change, Appl. Environ. Microb., 71, 2642–2652, 2005.

SAS Institute: The SAS System for Windows, Release 8.02, SAS Institute Inc., Cary, NC., 2001.

Ishizuka, S., Iswandi, A., Nakajima, Y., Yonemura, S., Sudo, S., Tsuruta, H., and Murdiyarso, D.: The variation of greenhouse gas emissions from soils of various land-use/cover types in Jambi province, Indonesia, Nutr. Cycl. Agroecosys., 71, 17–32, 2005.

Jaeger, C. H., Monson, R. K., Fisk, M. C., and Schmidt, S. K.: Seasonal partitioning of nitrogen by plants and soil microorganisms in an alpine ecosystem, Ecology, 80, 1883–1891, 1999.

Jang, I., Lee, S., Hong, J. H., and Kang, H. J.: Methane oxidation rates in forest soils and their controlling variables: a review and a case study in Korea, Ecol. Res., 21, 849–854, 2006.

Jiang, H., Apps, M. J., Peng, C. H., Zhang, Y. L., and Liu, J. X.: Modelling the influence of harvesting on Chinese boreal forest carbon dynamics, Forest Ecol Manag., 169, 65–82, 2002.

Kim, Y., Ueyama, M., Nakagawa, F., Tsunogai, U., Harazono, Y., and Tanaka, N.: Assessment of winter fluxes of CO_2 and CH_4 in boreal forest soils of central Alaska estimated by the profile method and the chamber method: A diagnosis of methane emission and implications for the regional carbon budget, Tellus B, 59, 223–233, 2007.

King, G. M. and Schnell, S.: Effect of Increasing Atmospheric methane concentration on ammonium inhibition of soil methane consumption, Nature, 370, 282–284, 1994.

Kleja, D. B., Svensson, M., Majdi, H., Jansson, P. E., Langvall, O., Bergkvist, B., Johansson, M. B., Weslien, P., Truusb, L., Lindroth, A., and Agren, G. I.: Pools and fluxes of carbon in three Norway spruce ecosystems along a climatic gradient in Sweden, Biogeochemistry, 89, 7–25, 2008.

Knorr, M., Frey, S. D., and Curtis, P. S.: Nitrogen additions and litter decomposition: A meta-analysis, Ecology, 86, 3252–3257, 2005a.

Knorr, W., Prentice, I. C., House, J. I., and Holland, E. A.: Long-term sensitivity of soil carbon turnover to warming, Nature, 433, 298–301, 2005b.

Lloyd, J. and Taylor, J. A.: On the temperature-dependence of soil respiration, Funct. Ecol., 8, 315–323, 1994.

Luo, Y. Q., Wan, S. Q., Hui, D. F., and Wallace, L. L.: Acclimatization of soil respiration to warming in a tall grass prairie, Nature, 413, 622–625, 2001.

Luyssaert, S., Schulze, E. D., Borner, A., Knohl, A., Hessenmoller, D., Law, B. E., Ciais, P., and Grace, J.: Old-growth forests as global carbon sinks, Nature, 455, 213–215, 2008.

Maljanen, M., Hytonen, J., and Martikainen, P. J.: Fluxes of N_2O, CH_4 and CO_2 on afforested boreal agricultural soils, Plant Soil, 231, 113–121, 2001.

McDowell, W. H., Magill, A. H., Aitkenhead-Peterson, J. A., Aber, J. D., Merriam, J. L., and Kaushal, S. S.: Effects of chronic nitrogen amendment on dissolved organic matter and inorganic nitrogen in soil solution, Forest Ecol. Manag., 196, 29–41, 2004.

Melillo, J. M., Steudler, P. A., Aber, J. D., Newkirk, K., Lux, H., Bowles, F. P., Catricala, C., Magill, A., Ahrens, T., and Morrisseau, S.: Soil warming and carbon-cycle feedbacks to the climate system, Science, 298, 2173–2176, 2002.

Merino, A., Perez-Batallon, P., and Macias, F.: Responses of soil organic matter and greenhouse gas fluxes to soil management and land use changes in a humid temperate region of southern Europe, Soil Biol. Biochem., 36, 917–925, 2004.

Micks, P., Aber, J. D., Boone, R. D., and Davidson, E. A.: Short-term soil respiration and nitrogen immobilization response to nitrogen applications in control and nitrogen-enriched temperate forests, Forest Ecol. Manag., 196, 57–70, 2004.

Mo, J., Zhang, W., Zhu, W., Gundersen, P., Fang, Y., Li, D., and Wang, H.: Nitrogen addition reduces soil respiration in a mature tropical forest in southern China, Glob. Change Biol., 14, 403–412, 2008.

Morishita, T., Sakata, T., Takahashi, M., Ishizuka, S., Mizoguchi, T., Inagaki, Y., Terazawa, K., Sawata, S., Igarashi, M., Yasuda, H., Koyama, Y., Suzuki, Y., Toyota, N., Muro, M., Kinjo, M., Yamamoto, H., Ashiya, D., Kanazawa, Y., Hashimoto, T., and Umata, H.: Methane uptake and nitrous oxide emission in Japanese forest soils and their relationship to soil and vegetation types, Soil Sci. Plant Nutr., 53, 678–691, 2007.

Nedwell, D. B. and Watson, A.: CH_4 production, oxidation and emission in a UK ombrotrophic peat bog : Influence of ${SO_4}^{2-}$ from acid-rain, Soil Biol. Biochem., 27, 893–903, 1995.

Odum, E. P.: Strategy of ecosystem development, Science, 164, 262–270, 1969.

Peng, S. S., Piao, S. L., Wang, T., Sun, J. Y., and Shen, Z. H.: Temperature sensitivity of soil respiration in different ecosystems in China, Soil Biol. Biochem., 41, 1008–1014, 2009.

Peterjohn, W. T., Melillo, J. M., Steudler, P. A., Newkirk, K. M., Bowles, F. P., and Aber, J. D.: Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures, Ecol. Appl., 4, 617–625, 1994.

Prescott, C. E., Kabzems, R., and Zabek, L. M.: Effects of fertilization on decomposition rate of Populus tremuloides foliar litter in a boreal forest, Can. J. Forest Res., 29, 393–397, 1999.

Prieme, A. and Christensen, S.: Seasonal and spatial variation of methane oxidation in a Danish spruce forest, Soil Biol. Biochem., 29, 1165–1172, 1997.

Rey, A., Pegoraro, E., Tedeschi, V., De Parri, I., Jarvis, P. G., and Valentini, R.: Annual variation in soil respiration and its components in a coppice oak forest in Central Italy, Glob. Change Biol., 8, 851–866, 2002.

Silver, W. L., Thompson, A. W., McGroddy, M. E., Varner, R. K., Dias, J. D., Silva, H., Crill, P. M., and Keller, M.: Fine root dynamics and trace gas fluxes in two lowland tropical forest soils, Glob. Change Biol., 11, 290–306, 2005.

Simpson, I. J., Edwards, G. C., Thurtell, G. W., den Hartog, G., Neumann, H. H., and Staebler, R. M.: Micrometeorological measurements of methane and nitrous oxide exchange above a boreal aspen forest, J. Geophys. Res.-Atmos., 102, 29331–29341, 1997.

Sitaula, B. K., Bakken, L. R., and Abrahamsen, G.: CH_4 uptake by temperate forest soil: Effect of N input and soil acidification, Soil Biol. Biochem., 27, 871–880, 1995.

Sotta, E. D., Veldkamp, E., Schwendenmann, L., Guimaraes, B. R., Paixao, R. K., Ruivo, M. D. L. P., Da Costa, A. C. L., and Meir, P.: Effects of an induced drought on soil carbon dioxide (CO_2) efflux and soil CO_2 production in an Eastern Amazonian rainforest, Brazil, Glob. Change Biol., 13, 2218–2229, 2007.

Sulzman, E. W., Brant, J. B., Bowden, R. D., and Lajtha, K.: Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO_2 efflux in an old growth coniferous forest, Biogeochemistry, 73, 231–256, 2005.

Suwanwaree, P. and Robertson, G. P.: Methane oxidation in forest, successional, and no-till agricultural ecosystems: Effects of nitrogen and soil disturbance, Soil Sci. Soc. Am. J., 69, 1722–1729, 2005.

Tang, X. L., Liu, S. G., Zhou, G. Y., Zhang, D. Q., and Zhou, C. Y.: Soil-atmospheric exchange of CO_2, CH_4, and N_2O in three subtropical forest ecosystems in southern China, Glob. Change Biol., 12, 546–560, 2006.

Teepe, R., Brumme, R., Beese, F., and Ludwig, B.: Nitrous oxide emission and methane consumption following compaction of forest soils, Soil Sci. Soc. Am. J., 68, 605–611, 2004.

Teh, Y. A., Silver, W. L., and Conrad, M. E.: Oxygen effects on methane production and oxidation in humid tropical forest soils, Glob. Change Biol., 11, 1283–1297, 2005.

Tessier, J. T. and Raynal, D. J.: Use of nitrogen to phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation, J. Appl. Ecol., 40, 523–534, 2003.

Townsend, A. R., Vitousek, P. M., and Trumbore, S. E.: Soil organic matter dynamics along gradients in temperature and land use on the island of Hawaii, Ecology, 76, 721–733, 1995.

van den Pol-van Dasselaar, A., van Beusichem, M. L., and Oenema, O.: Effects of soil moisture content and temperature on methane uptake by grasslands on sandy soils, Plant Soil, 204, 213–222, 1998.

Verchot, L. V., Davidson, E. A., Cattanio, J. H., and Ackerman, I. L.: Land-use change and biogeochemical controls of methane fluxes in soils of eastern Amazonia, Ecosystems, 3, 41–56, 2000.

Wang, C. K., Yang, J. Y., and Zhang, Q. Z.: Soil respiration in six temperate forests in China, Glob. Change Biol., 12, 2103–2114, 2006.

Wang, Y. S. and Wang, Y. H.: Quick measurement of CH_4, CO_2 and N_2O emissions from a short-plant ecosystem, Adv. Atmos. Sci., 20, 842–844, 2003.

Werner, C., Kiese, R., and Butterbach-Bahl, K.: Soil-atmosphere exchange of N_2O, CH_4 and CO_2 and controlling environmental factors for tropical rain forest sites in western Kenya, J. Geophys. Res.-Atmos., 112, D03308, doi:10.01029/02006jd007388, 2007.

Werner, C., Zheng, X. H., Tang, J. W., Xie, B. H., Liu, C. Y., Kiese, R., and Butterbach-Bahl, K.: N_2O, CH_4 and CO_2 emissions from seasonal tropical rainforests and a rubber plantation in Southwest China, Plant Soil, 289, 335–353, 2006.

Whalen, S. C. and Reeburgh, W. S.: Methane oxidation, production, and emission at contrasting sites in a boreal bog, Geomicrobiol. J., 17, 237–251, 2000.

WRB, I. W. G.: World Reference Base for Soil Resources 2006, 2006.

Xu, M. and Qi, Y.: Soil-surface CO_2 efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California, Glob. Change Biol., 7, 667–677, 2001.

Yu, G. R., Song, X., Wang, Q. F., Liu, Y. F., Guan, D. X., Yan, J. H., Sun, X. M., Zhang, L. M., and Wen, X. F.: Water use efficiency of forest ecosystems in eastern China and its relations to climatic variables, New Phytol., 177, 927–937, 2008.

Zerva, A. and Mencuccini, M.: Short-term effects of clearfelling on soil CO_2, CH_4, and N_2O fluxes in a Sitka spruce plantation, Soil Biol. Biochem., 37, 2025–2036, 2005.

Zhang, J. H., Han, S. J., and Yu, G. R.: Seasonal variation in carbon dioxide exchange over a 200-year-old Chinese broad-leaved Korean pine mixed forest, Agr. Forest Meteorol., 137, 150–165, 2006.

Zhang, W., Mo, J. M., Zhou, G. Y., Gundersen, P., Fang, Y. T., Lu, X. K., Zhang, T., and Dong, S. F.: Methane uptake responses to nitrogen deposition in three tropical forests in southern China, J. Geophys. Res.-Atmos., 113, D11116, doi:10.11029/12007jd009195, 2008.

Zheng, Z. M., Yu, G. R., Fu, Y. L., Wang, Y. S., Sun, X. M., and Wang, Y. H.: Temperature sensitivity of soil respiration is affected by prevailing climatic conditions and soil organic carbon content: A trans-China based case study, Soil Biol. Biochem., 41, 1531–1540, 2009.

Zhou, G. Y., Liu, S. G., Li, Z., Zhang, D. Q., Tang, X. L., Zhou, C. Y., Yan, J. H., and Mo, J. M.: Old-growth forests can accumulate carbon in soils, Science, 314, 1417–1417, 2006..