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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 actual 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 seasonal rain forest were selected along the eastern China. In each old-growth forest, soil CO_2 and CH_4 fluxes were measured for three years using the static chamber and gas chromatography technique. Soil temperature and moisture at the 10 cm depth were measured simultaneously 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 flux ranged from 18.09±0.22 to 35.40±2.24 Mg CO_2 ha^{-1} yr^{-1} and annual mean CH_4 flux ranged from −0.04±0.11 to −5.15±0.96 kg CH_4 ha^{-1} yr^{-1}. Soil CO_2 fluxes in the old-growth forests were mainly driven by soil temperature, followed by soil moisture and NO_3^--N. Based on the gradient theory of exchange of time and space, increase in air temperature in the future would promote soil CO_2 emission in the old-growth forests. The responses of soil CH_4 uptake to warming were dependent upon the critical temperature in forest. In addition, the NO_3^--N promotion to CO_2 emission could partially attribute to the compound effects of high nitrate stimulation on soil microbe activities and increased decomposability of organic materials. The mechanism of NH_4^+ inhibition to CH_4 uptake included both a competitive inhibition of CH_4 mono-oxygenase enzyme and a toxic inhibition by hydroxylamine or nitrite produced via NH_4^+ oxidation. Overall, increasing in precipitation and nitrogen deposition in eastern China would increase soil CO_2 emission, but decrease soil CH_4 uptake in the old-growth forests.

1 Introduction

Recently, some studies suggest that old-growth forests can continue to sequester carbon and serve as a global carbon dioxide sink (Zhou et al., 2006; Luyssaert et al., 2008). Most of the sequestered carbon dioxide is stored as slowly decomposing organic matter in litter and soil (Zhou et al., 2006). As an important process of C cycling, soil-atmospheric CO_2 and CH_4 exchanges 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 and precisely estimating carbon exchanges between the atmosphere and forest soils are critical to model prediction of trace gas fluxes. In the past two decades, studies on responses of soil-atmospheric C exchanges to climate change and N deposition in forests mostly focus 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 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 affect on (Prescott et al., 1999; McDowell et al., 2004) soil-atmospheric CO_2 and CH_4 exchanges. Also, the responses of soil respiration to warming include both promotion (Bergner et al., 2004) and acclimation (Luo et al., 2001; Melillo et al., 2002). To our knowledge, only few reports are available in literature on evaluation of the combination effects of multiple environmental factors on CO_2 and CH_4 fluxes from old-growth forest soils under natural conditions.

Environmental gradient method which can deal with a gradual and continuous change in time and space is widely used 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). In addition, the total deposition of atmospheric nitrogen peaked over the central South China, with maximum values of 63.5 kg N ha^{-1} yr^{-1} and an average value of 12.9 kg N ha^{-1} yr^{-1} (Lu and Tian, 2007). Zonal forest ecosystems, from the tropical rain forest in the south to the boreal coniferous forest in the north, along eastern China provide a unique research platform to investigate the effects of multiple environmental factors on soil-atmospheric CO_2 and CH_4 exchanges 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 from four primary old-growth forests in eastern China. Our specific aims are (1) to compare the difference of soil-atmospheric CO_2 and CH_4 exchanges in different forests; (2) to evaluate the relationship between soil-atmospheric CO_2 and CH_4 exchanges and soil temperature, moisture and soil mineral N (NH_4^+-N and NO_3^--N) concentrations.

2 Materials and methods

2.1 Study sites

Four old-growth forest sites are referred to as Daxinganling boreal coniferous forest, Changbaishan temperate needle-broadleaved mixed forest, Dinghushan subtropical evergreen broad-leaved forest, and Xishuangbanna tropic seasonal 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 a mean annual temperature of −5.4°C in the boreal forest to 21.4°C in the tropic 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, and then decreases to 18.1 kg N ha^{-1} yr^{-1} in the tropic. The boreal forest is a single forest with

Larix gmelinii as the predominant tree species (Jiang et al., 2002). The dominant vegetation species in the temperate forest are *Pinus koriaensis*, *Tilia amurensis*, *Acer mono*, *Quercus mongolica*, and *Fraxinus mandshurica* in the tree layer (Zhang et al., 2006). The major species in the subtropical forest are *Schima superba*, *Syzygium jambos*, *Castanopsis chinensis*, etc. in tree layers (Mo et al., 2008). The most abundant species in the tropical forest are *Pometia tomentosa*, *Terminalia myriocarpa*, *Myristica yunnanensis*, *Horsfieldia tetratepala*, *Homalium laoticum*, etc. (Werner et al., 2006). The soils are Brown coniferous forest soil, Dark brown soil, Lateritic red soil and Latosol (FAO/UNESCO taxonomy) from north to south, respectively. More extensive description on the sites was given in Table 1.

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 using static chamber and gas chromatography method (Wang and Wang, 2003). The static 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 square 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. A fan 10 cm in diameter was installed on the top wall of each chamber to make turbulence when chamber was closed. White adiabatic cover was added outside of the stainless steel cover to reduce the impact of direct radiative heating during sampling. The CO_2 effluxes were measured between 09:00 and 11:300 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 09:00 to 11:30 a.m. were close to daily means (Tang et al., 2006). The four gas samples were taken by 100 mL plastic syringes with 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 the rate of change in their concentration 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 greater than 0.95 in our study.

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

2.3 Soil sampling and mineral N analysis

In the middle ten days of each month during research, mineral soils nearby the gas chambers were taken from 0–10 cm depth using an auger (5 cm in diameter) after careful removal of O-horizon. Soil samples were not collected in non-growing season because soil frozen occurred from November to April next year at the boreal and temperate forest sites. Four samples were collected for each site. Soils were immediately passed through a 2 mm sieve to remove roots, gravel and stones. Soil sample was 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 Calculation of Q_{10}

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 (Eqs. 1 and 2) (Lloyd and Taylor, 1994):

$$R_s = R_0 e^{BT} \tag{1}$$

$$Q_{10} = R_{T+10}/R_T = e^{10B} \tag{2}$$

where, R_s is the soil respiration rate, T is the soil temperature, R_0 is the soil respiration rate as soil temperature is equal to zero, and B is regression coefficients.

2.5 Statistical analysis

A repeated measures analyses of variance (ANOVA) was performed on monthly means to test the difference of soil temperature, moisture, mineral N contents, and soil C fluxes by forests and seasons. Additionally, the relationships between CO_2 and CH_4 fluxes and soil properties (temperature, moisture and mineral N) were examined using 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.

3 Results

3.1 Seasonal variations of environmental conditions

Soil temperature and moisture showed clear seasonal courses (Fig. 2a). High soil temperature occurred at summer (July to September) and low soil temperature happened at winter (December to February). Soil moisture followed the same trends, high in summer and low in winter. However, the soil moisture did not show clear zonal differences from north to south as the soil temperature showed. In the boreal forest, the higher soil moisture content occurred around July (Fig. 2b). Similar phenomenon also occurred in the temperate forest (Fig. 2b). The seasonality of soil moisture was well consistent with the seasonal patterns of soil temperature in the tropical forests, that is, when the maximum soil moisture occurred in summer soil temperature also reached the highest (Fig. 2b). However, soil moisture in the subtropical forest decreased in summer months, whereas the soil temperature reached the maximum (Fig. 2b). Average monthly precipitation showed similar pattern as soil moisture in four old-growth forests

(Fig. 2c). Both in growing and non-growing season, there was significant difference for soil temperature and moisture between the four old-growth forests (Table 2).

3.2 Seasonality of soil mineral N

The NH_4^+-N concentration reached a maximum between April and May, and then followed by a substantial decrease at June in the tropical forest and a second NH_4^+-N peak appeared between July and August when soil temperature was high in the whole year (Fig. 3a). The similar variations were found in the boreal and temperate forests (Fig. 3a). However, the NH_4^+-N concentration remained relatively constant in subtropical forest in the whole year (Fig. 3a). In the growing season, there was significant difference for NH_4^+-N concentration among forests ($P<0.001$), with the averages (2003 to 2005) $12.78\pm0.52\,mg\,N\,kg^{-1}$ in boreal, $9.25\pm0.66\,mg\,N\,kg^{-1}$ in temperate, $2.75\pm0.13\,mg\,N\,kg^{-1}$ in subtropical and $22.63\pm0.43\,mg\,N\,kg^{-1}$ in tropical forest (Table 2).

In contrast, the NO_3^--N concentration varied greatly in the subtropical forest compared with other forest sites (Fig. 3b). The peaks of soil NO_3^--N in the subtropical site occurred between June and August, and the lower values usually occurred in winter and early spring (Fig. 3b). The change of NO_3^--N concentration showed a similar pattern in the tropical forest, where the higher NO_3^--N concentration appeared in warm July and August (Fig. 3b). However, in the boreal and temperate forests the NO_3^--N concentration tended to decrease with the time firstly and then slightly rose in the late growing season (Fig. 3b). From 2003 to 2005, the mean NO_3^--N concentrations in the growing season were significantly different among four old-growth forests, following the trend of the subtropical ($16.15\pm2.09\,mg\,N\,kg^{-1}$) > tropical ($7.46\pm0.10\,mg\,N\,kg^{-1}$) > temperate ($4.57\pm0.29\,mg\,N\,kg^{-1}$) > boreal ($2.01\pm0.19\,mg\,N\,kg^{-1}$) ($P<0.001$) (Table 2).

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3.3 Seasonality of CO_2 and CH_4 fluxes

Carbon dioxide emissions showed a consistent variation with soil temperatures, with the maximum in summer and minimum in winter for all forests (Fig. 4a). Seasonal differences of CO_2 emissions were more pronounced in the boreal and temperate forests than in the tropical and subtropical forests (Fig. 4a). Although total soil CO_2 emissions increased in the growing season ranging from 15.78 to 23.19 Mg CO_2 ha^{-1}, the differences among the four forests were not significant ($p>0.05$, Table 2). In the non-growing season, total CO_2 emissions in the boreal and temperature forests ranging from 2.31 to 3.28 Mg CO_2 ha^{-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} ($p<0.001$, Table 2).

Seasonality had significant impact on CH_4 emission and uptake. The higher uptake (i.e. negative CH_4 flux) and emission rates in the boreal and temperate forests were observed in summer and in winter, respectively (Fig. 4b). The subtropical forest soil behaved as net soil CH_4 uptake throughout the entire study period (Fig. 4b). There were significant differences for CH_4 fluxes between the growing and non-growing season for all four old-growth forests (Tables 2). In the non-growing season, the boreal forest behaved as CH_4 emission (0.78 kg CH_4 ha^{-1}) and the other three forests behaved as CH_4 uptake ranging from −1.18 to −3.66 kg CH_4 ha^{-1} (Table 2). However, in the growing season, only the tropical seasonal rain forest soil showed CH_4 emission with a mean of 1.18 kg CH_4 ha^{-1}, whereas the soil CH_4 uptake occurred in other forests ranging from −0.82 to −2.36 kg CH_4 ha^{-1} (Fig. 4b and Table 2).

3.4 Relationships between soil temperature, soil moisture and soil C fluxes

Soil CO_2 emission rate was fitted with soil temperature in an exponential model and the results indicate that soil temperature explained 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 (2.61) than in the tropical (2.16) and subtropical forests (2.05) (Table 3). Unlike the exponential relationship between CO_2 flux and soil temperature, CO_2 flux and soil moisture had a positive linear relationship, explaining 40–49% of CO_2 variations (Fig. 5b and Table 3). These results showed that soil CO_2 emission was mainly driven by soil temperature followed by soil moisture.

For all forest, there seems to be a critical temperature value by which the relationship between soil CH_4 flux and soil temperature changes from the negative to the positive when soil temperature raised above this temperature value (Fig. 5c). This critical value increased with decreasing latitude. For instance, the value was about 7–8°C in the boreal and temperate forests, 16 to 18°C in the tropical and subtropical forest (Table 3). If all four forests included in the model, the relationship between CH_4 flux and soil temperature was fitted well with Gaussian equation and the average critical soil temperate was 15°C (Fig. 5c and Table 3). Except in boreal forest, significant positive relationship between CH_4 flux and soil moisture was found in other forests, explaining 18–42% of CH_4 variations (Fig. 5d and Table 3). These results indicate that the response of soil CH_4 uptake to warming depends upon soil temperature and decreases with increasing precipitation in old-growth forests in eastern China.

3.5 Relationships 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 top 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 at the boreal and temperate forests (Fig. 6a and 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 occurs periodically, soil CH_4 flux was positively correlated to the NO_3^--N concentrations (Fig. 6d and Table 4). Taking all 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 revealed that soil NO_3^--N could promote soil CO_2 emission, while NH_4^+-N could inhibit CH_4 uptake in the old-growth forests in eastern China.

4 Discussions

4.1 Comparisons with other studies

The annual mean soil CO_2 emissions of 18.09 ± 0.22 and 20.08 ± 1.20 Mg CO_2 ha^{-1} yr^{-1}, respectively from the boreal and temperate forests (mean ± se) fall in the range of soil CO_2 emission rates of 11.59 to 40.15 Mg CO_2 ha^{-1} yr^{-1} reported by a number of studies worldwide (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 emission of 35.40±2.42 and 34.54±4.99 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 Mg CO_2 ha^{-1} yr^{-1}, Townsend et al., 1995) and in a tropical monsoon forest in Tainland (25.6 Mg CO_2 ha^{-1} yr^{-1}, Hashimoto et al., 2004), but lower than that in subtropical moist forest, Queensland, Australia (51.07 Mg CO_2 ha^{-1} yr^{-1}, Butterbach-Bahl et al., 2004) and tropical forests of South America (36.94–52.68 Mg CO_2 ha^{-1} yr^{-1}, Garcia-Montiel et al., 2004; Sotta et al., 2007).

The old-growth forest soils in eastern China represented efficient CH_4 uptake 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 growing season (−0.82 ± 0.03 kg CH_4 ha^{-1}), but emitted CH_4 when soils were frozen in the non-growing season (0.78 ± 0.13 kg CH_4 ha^{-1}). This result was the same as that (-1.04–4.95 kg CH_4 ha^{-1} yr^{-1}) found in typical boreal forest soils, 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 the uptake in the growing and as the emission in the non-growing season, respectively. Our data in the temperate forest were in the same range (−2.00∼−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 uptakes in the tropical and subtropical forest soils are comparable with that of other tropical forest soils (−2.10∼−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, 2007).

4.2 Effects of soil temperature and soil moisture on soil C fluxes

Based on the relationship between CO_2 emission and soil temperature and moisture, we can deduce that increasing air temperature and precipitation would increase soil CO_2 emission in the old-growth forests in eastern China in the future. The fact that no significant difference of soil CO_2 fluxes among the four old-growth forests in the growing season rather than the non-growing season indicates that the response of soil CO_2 emission to soil temperate was weak in higher than in lower temperature conditions. This phenomenon was comparable with the acclimation of soil respiration to elevated temperature in some warming experiments (Luo et al., 2001; Melillo et al., 2002). Additionally, some studies found that soil CO_2 emission increased with increasing soil moisture when soil moisture was within a site-specific threshold value, generally up to 60% water-filled pore space (WFPS) (Xu and Qi, 2001; Rey et al., 2002). In our study, soil moisture contents across all four forest sites were generally less than 50% (w/w) in the whole year (Fig. 5b and d), which was equivalent to 55% of WFPS calculated from the equation described by Franzluebbers (1999).

Some studies suggested that CH_4 oxidation was usually less sensitive to soil temperature than to soil moisture (Price et al., 2004; Jang et al., 2006; Werner et al., 2006), and the effect of temperature was much weaker on CH_4 oxidation than on CH_4 production since methanotrophs have high affinity for CH_4 in air and low activation energy for CH_4 oxidation (Dunfield et al., 1993; Castaldi and Fierro, 2005; Borken et al., 2006).

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 the critical temperature. The critical 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 lower than the critical temperature, the CH_4 and O_2 diffusion rates are greater than soil CH_4 and O_2 consumption rates due to low soil microbial activities. Consequently, the ability of forest soils to oxidize CH_4 is strongly correlated with soil temperature (Peterjohn et al., 1994; Nedwell and Watson, 1995; Prieme and Christensen, 1997). However, if soil temperature continually rises to superior the critical 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 fluxes and soil NO_3^--N concentrations across four forests suggests that NO_3^--N input from N deposition 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 poor-N natural forest ecosystems (Jaeger et al., 1999). Therefore, the higher soil NO_3^--N concentration, the more total and fine root biomass of forests will be (Table 1); accordingly, this could partially contribute to the higher autotrophic respiration. However, excessive reactive N input will result in occurrence of ecosystem N saturation and decrease of fine root biomass, which will decrease soil respiration (Mo et al., 2008). Therefore, we might deduce that old-growth forest ecosystem in subtropical region would be in N unsaturated status without excessive input of atmospheric N deposition.

High soil NO_3^--N content could 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 and b). This could be partially attributed to microbial immobilization of soil available N. Soil microbe needs 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 promoted soil respiration in N-limited forest ecosystems (Micks et al., 2004; McDowell et al., 2004).

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 forests suggests that elevated soil NH_4^+-N content from N deposition could significantly inhibit methane oxidation. This result was consisted with findings in many N addition experiments that adding N decreased CH_4 uptake from 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). Whalen et al. (1992) also estimated that the atmospheric N deposition could decrease forest soil CH_4 oxidation by 0.91 Tg CH_4 yr^{-1} globally. High concentration of soil NH_4^+-N could significantly inhibit methanotrophic activities in soils because it stimulated the quantity of NH_4^+-oxidizer bacteria in the organic layers of forest soil (King and Schnell, 1994; Whalen and Reeburgh, 2000). Both CH_4 oxidation and ammonium oxidation are controlled by monooxygenase enzymes, (soluble or particulate) methane monooxygenase, and ammonium monooxygenase, respectively, which all require O_2 (Hanson and Hanson, 1996) or alternate electron acceptors such as Fe^{3+}, NO_3^- and SO_4^{2-} (Dale et al., 2006).

However, the positive relationship between soil NO_3^--N and soil CH_4 flux in the tropical and boreal forest sites was inconsistent with other studies (Dunfield et al., 1995;

Corton et al., 2000). Corton et al. (2000) noted that $(NH_4)_2SO_4$ addition could inhibit methane production, but $NaNO_3$, KNO_3 and urea have either transitory or no effect on CH_4 production. We deduced that this effect could result from the anaerobic environment in boreal forest in winter due to soil frozen and in tropical forest in rain season due to waterlogging. In addition, 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 sensitivity of CO_2 flux to soil temperature (Q_{10}) tended to increase with the latitude. Considering the relationship of soil CO_2 emission to soil temperature, moisture and mineral N contents across forests, we can speculate that CO_2 fluxes between forest soils and the atmosphere will increase with increase in air temperature, precipitation and N deposition in the future. Moreover, the mechanism of NO_3^--N interaction with CO_2 emission could partially attribute to the compound effects of the stimulation of soil microbe activity to consume available C and the increased decomposability of organic materials due to decline in C/N ratio through N immobilization. The responses of soil CH_4 uptake to soil temperature vary with forest type, mainly dependent upon the critical temperature at each forest site. However, increasing precipitation and NH_4^+-N will decrease soil CH_4 uptake in the old-growth forests in eastern China. The mechanism of NH_4^+ inhibition on methane oxidation could include both a competitive inhibition of CH_4 mono-oxygenase enzyme and a toxic inhibition by hydroxylamine or nitrite produced via NH_4^+ oxidation.

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Table 1. Descriptions of the four old-growth forest ecosystem sites.

Sites	Daxinganling [a]	Changbai shan [a]	Dinghushan [a,b]	Xishuang banna[a,c]
Forest type	Boreal coniferous forest	Temperature mixed forest	Subtropical evergreen broadleaved forest	Tropic seasonal 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	67.2	87.7	73.5
Fine root biomass (Mg C ha^{-1})	2.40	2.82	4.90	3.06
Litter input (Mg C ha^{-1} yr^{-1})	2.50	4.52	8.42	11.56
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	11.5	8.8	7.53
Total N (g kg^{-1})	1.83	1.18	2.5	1.45
C/N	25.14	21.84	12.8	11.33
Soil pH	6.03	5.85	3.80	4.75

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

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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 sites	Soil temperature (°C)[f]		Soil moisture (%)		NH_4^+-N content ($mg\,kg^{-1}$)		NO_3^--N content ($mg\,kg^{-1}$)		Soil CO_2 flux ($MgCO_2\,ha^{-1}$)		Soil CH_4 flux ($kg\,CH_4\,ha^{-1}$)[e]	
	non-growing	growing	non-growing	growing	non-growing	growing	non-growing	growing	non-growing	growing	non-growing	growing
Boreal	−5.75 (0.75) C	8.15 (1.10) D	17.07 (2.15) B	36.88 (1.30) 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
Tempe-rate	−1.71 (0.61) B	12.29 (0.98) C	25.87 (3.29) A	42.25 (4.31) 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	20.71 (2.29) AB	29.75 (1.76) 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	22.27 (2.16) AB	39.77 (1.06) 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

[e] Negative CH_4 values are CH_4 uptake. [f] Means followed by different letters in the same column are significantly different (Turky's HSD comparison).

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

Forest	a	b	T_0^g	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	11.16		<0.0001	0.45	157.59	
Temperate	−29.62	7.56		<0.0001	0.49	140.35	
Subtropical	67.63	13.29		<0.0001	0.49	132.60	
Tropical	146.44	7.96		<0.0001	0.40	113.69	
All forests	72.03	8.06		<0.0001	0.29	172.03	
(c) $F_{CH_4}=a^*\exp(-0.5^*((T-T_0)/b)^2)$							
Boreal	−0.05	2.53	7.30	0.04	0.17	0.04	
Temperate	−0.04	4.19	7.78	0.004	0.31	0.03	
Subtropical	−0.07	9.25	17.98	0.004	0.82	0.03	
Tropical	−0.11	2.70	15.67	0.0003	0.61	0.05	
All forests	−0.05	8.25	15.25	<0.0001	0.37	0.05	
(d) $F_{CH_4}=a+b^*\ M$							
Boreal	0.04	−0.002		0.002	0.25	0.035	
Temperate	−0.02	0.0003		0.063	0.18	0.033	
Subtropical	−0.09	0.001		0.008	0.19	0.027	
Tropical	−0.17	0.005		<0.0001	0.42	0.063	
All forests	−0.05	0.007		0.0134	0.28	0.048	

[g] T_0 is the critical soil temperature at which soil CH_4 oxidation rates reach the maximum values.

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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

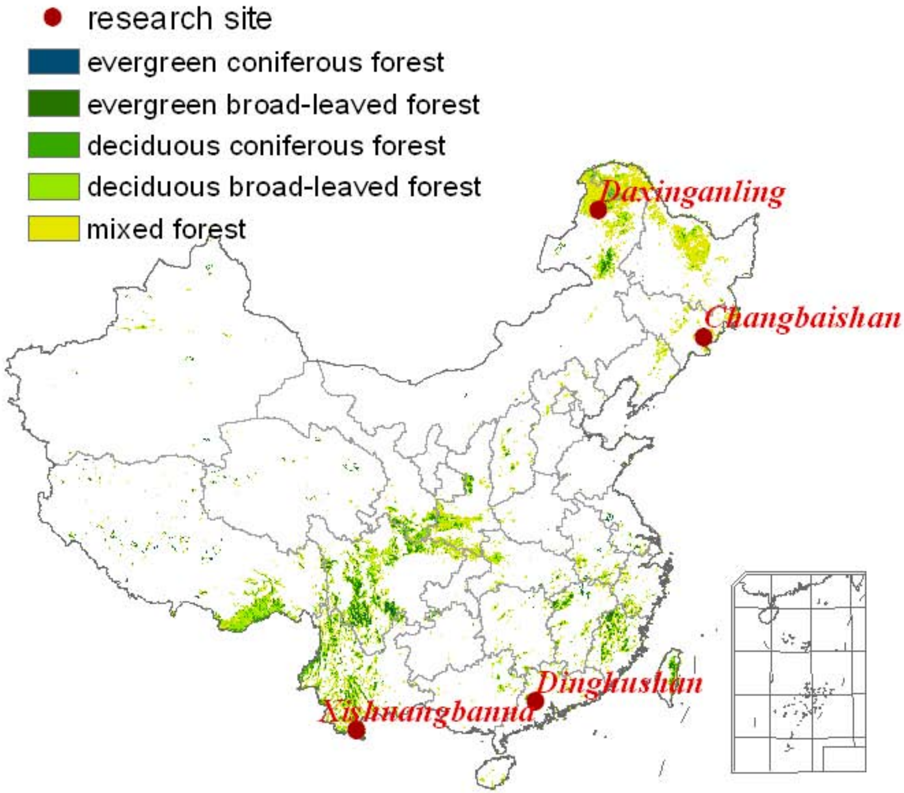

Fig. 1. Spatial distribution of soil CO_2 and CH_4 fluxes measurement sites in Eastern China.

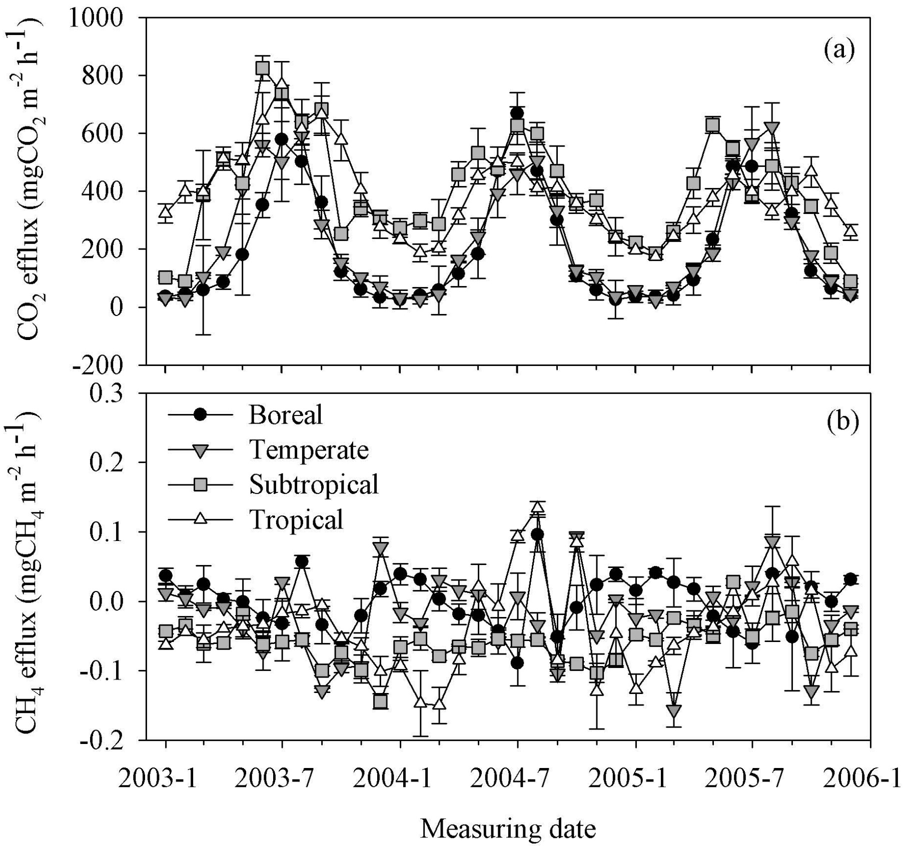

Fig. 2. The seasonal variation of soil temperature and moisture (±1 SE) at depth of 10 cm and average precipitation in four old-growth forests from 2003 to 2005.

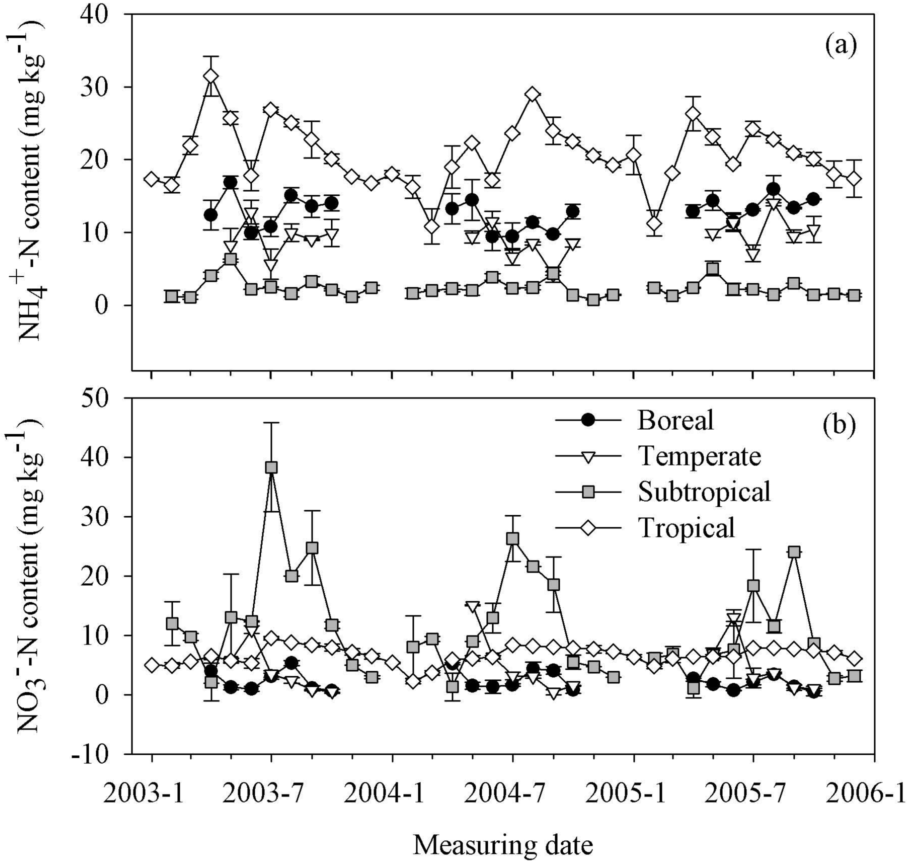

Fig. 3. The seasonal variation of soil NH_4^+-N and NO_3^--N concentrations (±1 SE) at depth of 10 cm in four old-growth forests from 2003 to 2005.

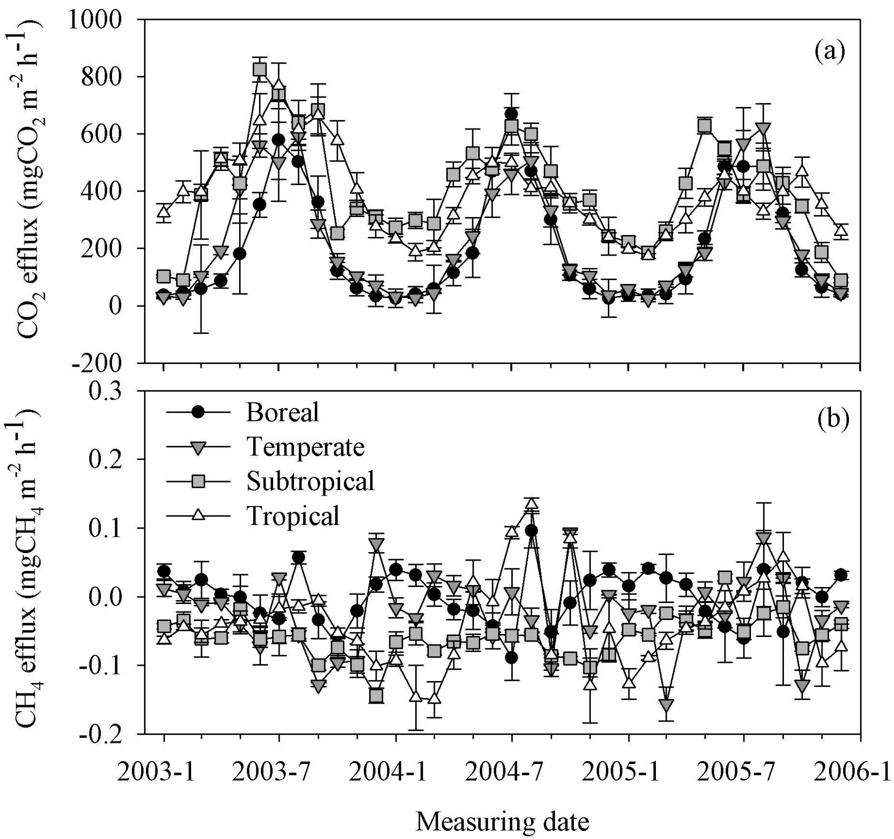

Fig. 4. Seasonal patterns of CO_2 and CH_4 fluxes (±1 SE) measured in four old-growth forests.

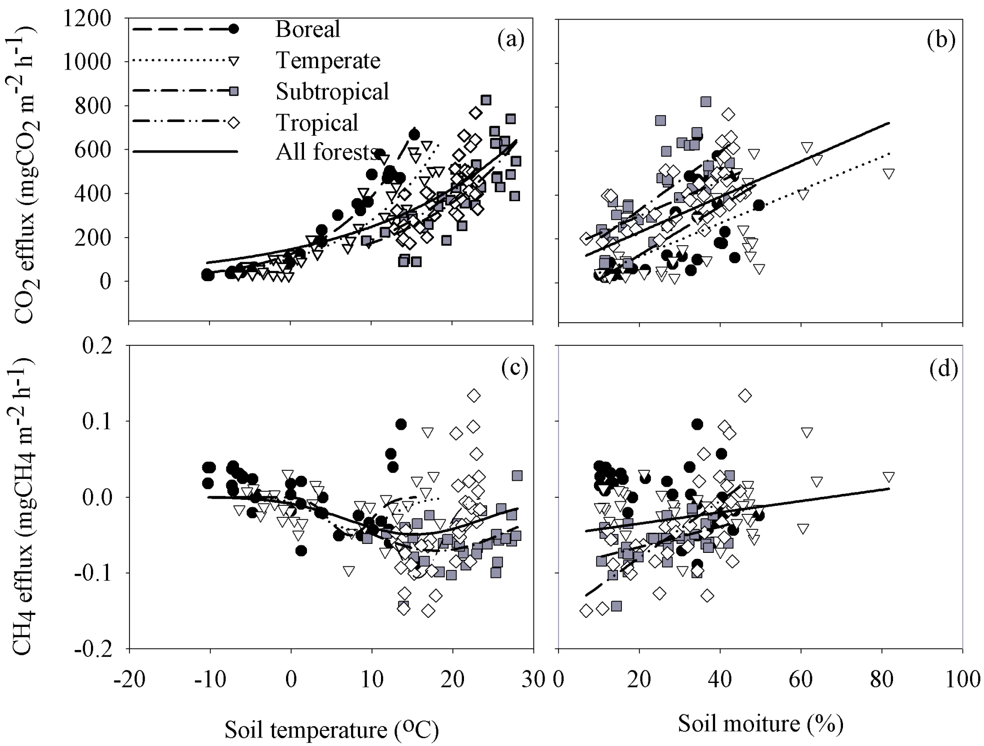

Fig. 5. Relationships of CO_2 and CH_4 fluxes to soil temperature and moisture at 10 cm below surface in the four forests.

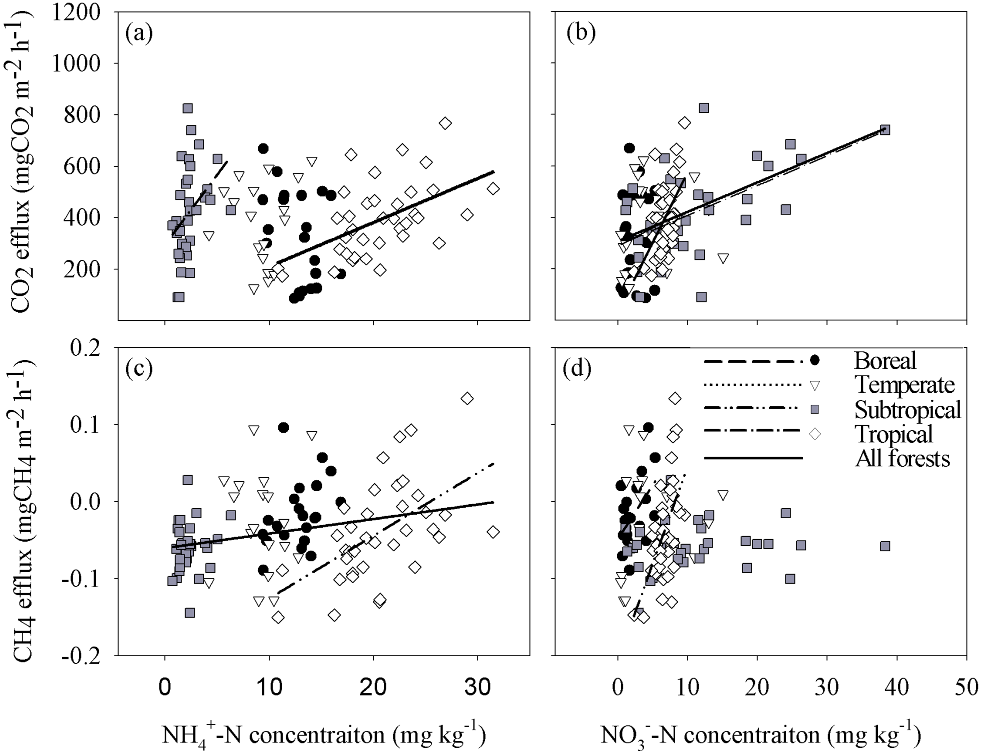

Fig. 6. Relationships of CO_2 and CH_4 fluxes to soil NH_4^+-N and NO_3^--N at 10 cm below surface in the four forests.

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