The litter layer acts as a moisture-induced bidirectional buffer for atmospheric methane uptake by soil of a subtropical pine plantation

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Yidong Wang [a,b], Huimin Wang [a,*], Zeqing Ma [a], Xiaoqin Dai [a], Xuefa Wen [a], Yunfen Liu [a], Zhong-Liang Wang [b]

[a] Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China
[b] Tianjin Key Laboratory of Water Resources and Environment, Tianjin Normal University, Tianjin 300387, China

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ABSTRACT

Forest soils are well known sinks for atmospheric methane (CH$_4$), but how the surface litter layer controls gas diffusion into the mineral soil is still unclear. Seasonal rainfall in the humid climate provides a unique opportunity to examine uptake of atmospheric CH$_4$ under a wide range of soil water content (SWC). We studied this question using a litter removal method in a 20-year-old slash pine (*Pinus elliottii*) plantation in subtropical China during 2005–2007. Soil-atmosphere CH$_4$ fluxes of the control (F_{CK}) and litter-free (F_{LF}) treatments and their differences (litter-affected CH$_4$ flux, $F_{CK-LF} = F_{CK} - F_{LF}$) were all significantly influenced by SWC and not by soil temperature. Litter layer reduced atmospheric CH$_4$ uptake by soil when SWC was below 15.8 vol%, and increased atmospheric CH$_4$ consumption by soil when SWC was above this value. We concluded that the litter layer acts as a moisture-induced bidirectional buffer for atmospheric CH$_4$ uptake by soils in a subtropical humid pine plantation. However, the removal of the litter layer had a minimal effect (+0.7%) on annual atmospheric CH$_4$ uptake by soil, through compensating effects during the wet and dry seasons. Therefore, in the context of climate change, future changes in SWC will alter the strength of atmospheric CH$_4$ uptake by soils of subtropical pine plantations.

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1. Introduction

Methane (CH$_4$) is the second most important anthropogenic greenhouse gas, contributing approximately 14% to global warming (IPCC, 2007). Moreover, methane plays an important role in changing the chemical composition of the atmosphere (Cicerone and Oremland, 1988). The main route for removing atmospheric CH$_4$ is through reactions with hydroxyl radicals in the troposphere. Atmospheric CH$_4$ uptake by aerobic soils through microbial oxidation is a secondary sink and is large enough (about 30 Tg year^{-1}) to influence the global CH$_4$ budget, and this uptake is likely to shift with changes associated with climate change and human activities (Smith et al., 2000; Le Mer and Roger, 2001; IPCC, 2007).

Forested soils are the largest active biotic sinks for atmospheric CH$_4$ on an areal basis (Smith et al., 2000; Le Mer and Roger, 2001). Atmospheric CH$_4$ uptake strength by aerated soils is usually controlled by methanotrophs (CH$_4$ oxidizing microbes) and gas diffusivity. Methanotrophs generally have their highest activity in the uppermost mineral layers (Bender and Conrad, 1994; Price et al., 2003; Wolf et al., 2011) due to lower amounts of ammonium (Schnell and King, 1994) and more favorable soil water content (SWC) (Schnell and King, 1996). Because of the high potential of CH$_4$ oxidation by methanotrophs (Saari et al., 1998), gas diffusivity is generally the primary factor in regulating atmospheric CH$_4$ consumption in forest soils (Striegl, 1993; Brumme and Borken, 1999). Gas diffusivity is greatly affected by SWC, as CH$_4$ diffuses 10^4 times slower in water than in air (Marrero and Mason, 1972). Litter layers of boreal and temperate well drained forests have generally been reported to have little CH$_4$ oxidation capacities (Saari et al., 1998; Brumme and Borken, 1999; Steinkamp et al., 2001). Thus, litter layers are primarily considered as physical barriers against atmospheric CH$_4$ diffusion to mineral soils. Reductions in atmospheric CH$_4$ uptake by soil (Brumme and Borken, 1999), especially under dry soil conditions, have been shown in litter removal studies (Borken and Brumme, 1997; Dong et al., 1998; Saari et al., 1998; Steinkamp et al., 2001; Price et al., 2003; Yan et al., 2008; Peichl et al., 2010). In support of this concept, Brumme and Borken (1999) found a negative relationship between CH$_4$ uptake rates and thickness of organic horizons. However, Borken and Beese

* Corresponding author. Tel./fax: +86 10 64888896.
  E-mail address: wanghm@igsnrr.ac.cn (H. Wang).

(2006) suggested that litter layer removal decreased CH_4 uptake by German forest soils because the litter horizon may hold partial rainfall and maintain gas diffusivity of the mineral soil. Furthermore, in contrast to boreal and temperate forests, litter layers of tropical montane forests have high CH_4 methane oxidation rate, which can influence CH_4 exchange between the soil and atmosphere (Wolf et al., 2011). Thus, under wet soil conditions, litter layers may also mitigate mineral soil water saturation and increase atmospheric CH_4 uptake by soils and litter layers.

Subtropical forests of southern China are characterized by a humid climate with high temperatures and precipitation rates. Even though annual rainfall is relatively high, seasonal wet (January–June) and dry (July–December) conditions alternate over an annual cycle. It is not known how this precipitation regime affects atmospheric CH_4 consumption by subtropical forest soils. With climate change induced changes in precipitation amount and patterns, we need a better understanding of the potential bidirectional buffering roles of litter layer on CH_4 uptake by forest soils. Furthermore, subtropical forests are widely distributed and currently encompass a total area of approximately 53 million hectares. By the late 1970s, however, the majority of natural forests, primarily composed of evergreen broad-leaved species, were heavily destroyed. To prevent environmental degradation, forest restoration campaigns were extensively launched in the 1980s (Wang et al., 2011, 2012b). These forest plantations, which accounted for 41% of the total subtropical forested area, were mainly established by coniferous species. Slash pine (*Pinus elliottii*) is an important member of the conifers due to its fast growth characteristic (Wang et al., 2009, 2012a). Nevertheless, it is not clear how litter layer affects atmospheric CH_4 uptake by soils of subtropical humid slash pine plantations in southern China.

The objectives of this study were to test the following hypotheses: (*i*) the litter layer will reduce atmospheric CH_4 uptake by soil under dry conditions, (*ii*) the litter layer may promote atmospheric CH_4 consumption by soil under wet conditions, (*iii*) the bidirectional buffering effects will be regulated by soil moisture, and (*iv*) the balance of the bidirectional buffering effects determine the annual role of litter layer on atmospheric CH_4 uptake by soil of slash pine plantations in subtropical China.

2. Materials and methods

2.1. Site description

This research was carried out in an evergreen slash pine (*P. elliottii* Englem.) plantation (26°44′39″ N, 115°03′33″ E, elevation 102 m) at Qianyanzhou Ecological Research Station in subtropical China. This even-aged pine plantation was established in 1985. There were also a few Masson pine (*Pinus massoniana*) in this stand. Mean tree height was 15 m; mean diameter at breast height was 16.1 cm; mean stand basal area was 35 m^2 ha^{-1}; and mean leaf area index was 4.5 m^2 m^{-2}. The main understory and midstory species were *Woodwardia japonica* (L. f.) Sm., *Dicranopteris dichotoma* (Thunb.) bernh, *Loropetalum chinense* (R. Br.) Oliver., and *Quercus fabric* Hance. Prior to being a pine plantation, the vegetation was dominated by shrubs and grasses. The soil, weathered from red sandstone and mud stone, is common for this region and classified as a Typic Dystrudepts using the soil taxonomy of United States Department of Agriculture. Soil texture was sandy loam with 68% sand and 15% clay (Wen et al., 2010). Surface (0–20 cm) bulk density was 1.51 g cm^{-3}; porosity was 43%; organic carbon was 9.4 g kg^{-1}; total N content was 0.66 g kg^{-1}; and pH was 4.5. This area was characterized by a humid monsoon climate, with a mean air temperature of 17.9 °C, rainfall amounts of 1469 mm $year^{-1}$ and rainfall frequency of 75–100 days $year^{-1}$ (1985–2008). Annual

evapotranspiration was 747 mm $year^{-1}$ (2003–2007; Wen et al., 2010). Even though annual precipitation is high, a seasonal drought (July–December) usually occurs. About 30% of precipitation and 54% of evapotranspiration occurred in the dry season during the period of 2003–2010. Further details can be found in Wang et al. (2011) and Zhang et al. (2011).

2.2. Experimental design

The litter layer of the slash pine plantation was approximately 4–5 cm in thickness, with a carbon density of about 900 g C m^{-2}. We used a litter layer removal method (Wang et al., 2012b) to investigate the impact of litter layer on soil-atmosphere CH_4 flux. The treatments of soil with and without litter layer were defined as control and litter-free, respectively. Each treatment had six sampling points, located about 3–5 m apart. The two treatments were laid out using a pairwise distribution. All chambers were placed at some distance (>1 m) from the tree stems to avoid cutting coarse roots. In the litter-free treatment, nylon nets (2–mm mesh) were placed on the soil surface in order to conveniently remove fresh litter. Litter was removed one or two days before measurement. The ground shrubs and grasses in both treatments were removed during the whole study period.

2.3. Measurement of soil-atmosphere CH_4 flux

Soil-atmosphere CH_4 fluxes of the control (F_{CK}) and litter-free (F_{LF}) treatments were measured using a closed, static and opaque chamber-gas chromatography system (Wang et al., 2012a, b). Flux measurements were carried out between 9:00–11:00 a.m. approximately twice a week from January 2005 to December 2007. During September–October 2007, flux measurements were intermittent due to an instrument problem. The litter-based CH_4 flux ($F_{CK–LF}$) was calculated as the difference between F_{CK} and F_{LF}: $F_{CK–LF} = F_{CK} − F_{LF}$. Twelve permanent bases (50 × 50 cm) with troughs made of stainless steel were inserted into the mineral soil to approximately 3 cm deep. Chamber bases were installed more than 3 months prior to the first measurements. The stainless steel chambers (50 × 50 × 50 cm) were covered with cotton pads on the outside to reduce heat exchange between the inside of the chamber and the surrounding environment. The base troughs were filled with water to prevent air exchange between the inside and outside of the chamber. Two small electric fans were fixed at the opposite top corners of each chamber for air mixing. About 100 mL of gas were sampled immediately after the chamber closure using a gas-tight syringe through an F46-tube. Subsequently, four additional samples were collected every 10 min. CH_4 concentration of each sample was measured within two days using a gas chromatography instrument (Agilent 4890D; Agilent Technologies, Inc., Wilmington, Delaware, United States) equipped with a flame ionization detector (FID). Chromatographic separations were run using a stainless steel column (2 m long with a diameter of 2 mm) packed with 13XMS (60–80 mesh). The temperatures of the injection/detection and column oven were 200 and 55 °C, respectively. Ultra pure N_2 was used as the carrier gas at a rate of 30 mL min^{-1}. The limit of methane detection was 0.080 ± 0.008 μL L^{-1}. A certified methane standard with a concentration of 4.81 μL L^{-1} (China National Research Center for Certified Reference Materials, Beijing, China) was used for calibration. Soil-atmosphere CH_4 fluxes were calculated according to Eq. (1), and further calibrated with changes in temperature and pressure based on Eq. (2).

$$F = \frac{\Delta m}{A \cdot \Delta t} = \frac{V \cdot \Delta c}{A \cdot \Delta t} \tag{1}$$

$$F = \frac{V}{A} \cdot \frac{P}{P_0} \cdot \frac{T_0}{T} \cdot \frac{\Delta c}{\Delta t} \qquad (2)$$

where F is soil-atmosphere CH_4 flux ($\mu g\ CH_4\ m^{-2}\ h^{-1}$); Δm refers to increased CH_4 in the chamber (μg); A represents ground area covered by the chamber (m^2); Δc and Δt are changes of CH_4 content ($\mu g\ m^{-3}$) and elapsed time (h) from chamber closure to gas sampling, respectively; V refers to the volume of the chamber (m^3); T and P are air temperature (K) in the chamber and pressure (kPa) of the surrounding environment at the sampling time, respectively; and T_0 (273 K) and P_0 (101.3 kPa) are temperature and pressure, respectively, under standard condition. Occasionally, data from individual chambers was excluded if changes in CH_4 concentrations did not follow a constant linear increase or decrease ($R < 0.9$).

2.4. Measurement of environmental factors

Concomitantly with CH_4 flux measurement, air temperature inside the static chamber was measured using thermocouples (JM624; Jinming Instruments Co. Ltd., Tianjin, China). Atmospheric pressure was monitored using an atmospheric pressure sensor (CS105; Vaisala Inc., Woburn, Massachusetts) fixed on a flux tower near the study site. Soil temperature (T_S) and volumetric SWC at 5 cm depth were measured simultaneously with CH_4 flux observations using a portable thermocouple (JM624) and a time domain reflectometer (TDR) (TSC-I; China Agricultural University, Beijing, China), respectively. Rainfall was measured continuously with a rain gauge (TE525MM; Campbell Scientific Inc., United States) installed over the canopy on the flux tower, about 20 m away from the location of the chambers.

2.5. Data analysis

The dependences of soil-atmosphere CH_4 flux on soil temperature and water content were simulated using Eq. (3). The dependences of soil CH_4 flux on both T_S and SWC were modeled using Eq. (4).

$$F = \alpha \ln x + \beta \qquad (3)$$

$$F = \alpha \ln T_S + \beta \ln SWC + \gamma \qquad (4)$$

where F is measured soil-atmosphere CH_4 flux ($\mu g\ CH_4\ m^{-2}\ h^{-1}$); x is soil temperature (°C) or volumetric water content (vol%); T_S refers to soil temperature (°C); SWC is volumetric soil water content (vol%); α, β and γ are the fitted parameters. Correlations between soil-atmosphere CH_4 flux and natural logarithms of T_S and SWC were performed with SPSS 13.0 (SPSS Inc., Chicago, Illinois, United States). Figures were drawn using ORIGIN 8.0 (OriginLabs Corporation, Northampton, Massachusetts, United States) and CorelDraw 9 (Corel Corporation, Canada).

3. Results

3.1. Temporal CH_4 flux and environmental factors

During the study period of 2005–2007 (Fig. 1 a), F_{CK} varied from −67.2 to +21.1 $\mu g\ CH_4\ m^{-2}\ h^{-1}$, with an average of −14.3 $\mu g\ CH_4\ m^{-2}\ h^{-1}$ (negative values indicate uptake). F_{LF} ranged from −90.4 to +34.0 $\mu g\ CH_4\ m^{-2}\ h^{-1}$, with an average of −14.2 $\mu g\ CH_4\ m^{-2}\ h^{-1}$. F_{CK-LF} varied from −45.5 to +52.5 $\mu g\ CH_4\ m^{-2}\ h^{-1}$, with an average of −0.1 $\mu g\ CH_4\ m^{-2}\ h^{-1}$ (Fig. 1b). Monthly mean F_{CK} and F_{LF} had general seasonal fluctuations, with low uptake values
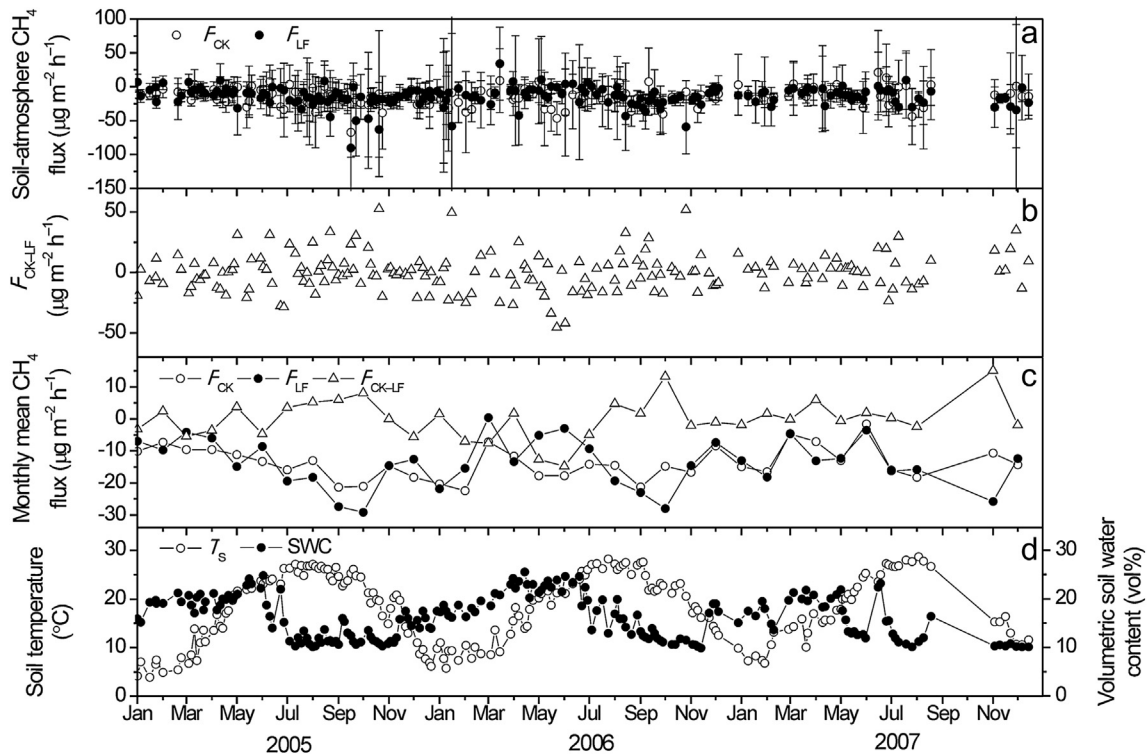

Fig. 1. Soil-atmosphere CH_4 fluxes (negative values indicate atmospheric CH_4 uptakes by soil) and environmental variables during the period of 2005–2007: (a) CH_4 fluxes of the control (F_{CK}) and litter-free (F_{LF}) treatments; (b) litter-affected CH_4 flux ($F_{CK-LF} = F_{CK} - F_{LF}$); (c) monthly mean F_{CK}, F_{LF} and F_{CK-LF}; and (d) soil temperature and moisture. In subfigure (a), each value refers to the average of six measurements and error bars represent the standard deviations.

during the wet season (January–June) and high uptake values during the dry season (July–December) (Fig. 1c). In contrast, monthly mean F_{CK-LF} had a generally reversed pattern (Fig. 1c). Soil temperature varied from 3.9 to 28.7 °C, with an average of 18.5 °C (Fig. 1d). Mean SWC during the wet seasons and the dry seasons was 19.5 and 12.9 vol%, respectively (Fig. 1d).

3.2. Dependence of CH₄ flux on soil temperature and moisture

Monthly mean F_{CK} and F_{LF} were not affected by T_S ($P = 0.40$ and 0.21, respectively) (Fig. 2a). Monthly mean F_{CK-LF} was also not influenced by T_S ($P = 0.40$) (Fig. 2a). In contrast, monthly mean F_{CK} and F_{LF} were positively related with SWC (Fig. 2b). However, monthly mean F_{CK-LF} was negatively influenced by SWC and reached zero when SWC was about 15.8 vol% (Fig. 2b). This indicates that the litter layer negatively affected CH₄ uptake when SWC was below 15.8 vol% and positively affected CH₄ uptake when SWC was above this value (Fig. 2b). Due to the co-effects of T_S and SWC, both variables were used to model F_{CK}, F_{LF} and F_{CK-LF}, but precision of the simulations was not improved.

3.3. CH₄ uptake during the wet and dry seasons

Monthly mean F_{CK}, F_{LF} and F_{CK-LF} were not affected by T_S during both the wet and dry seasons ($P = 0.24–0.66$) (Fig. 3 a and b). During the wet seasons, F_{CK}, F_{LF} and F_{CK-LF} were not influenced by

SWC ($P = 0.06–0.38$) (Fig. 3c). In contrast, during the dry seasons, F_{LF} and F_{CK-LF} were both correlated to SWC ($P = 0.02$ and 0.03) (Fig. 3d).

3.4. Annual soil CH₄ uptake and the effect of litter layer

According to the annual mean CH₄ flux (Fig. 1), the cumulative annual CH₄ uptake by the control and litter-free soils was estimated to be 125.0 ± 31.9 and 124.2 ± 28.6 mg CH₄ m^{-2} year^{-1}, respectively, suggesting that litter layer had a minimal effect (+0.7%) on annual CH₄ uptake amount. Therefore, the bidirectional buffering effects of litter layer were offset by each other.

4. Discussion

4.1. Soil-atmosphere CH₄ flux and controlling factors

The net CH₄ exchange between soils and atmosphere is the balance between CH₄ production (methanogenesis) and consumption (methanotrophy). Forest soils are considered active sinks of atmospheric CH₄ (Smith et al., 2000; Le Mer and Roger, 2001). In this study, soils both with and without litter layers were generally CH₄ sinks. However, transient CH₄ sources were observed, especially during the wet seasons (Fig. 1 a). This result is in agreement with that in tropical rain forests (Davidson et al., 2004; Yan et al., 2008). Oxygen limitation (Verchot et al., 2000; Davidson et al., 2004) or consumption in decaying litter and upper soil organic matter (Maljanen et al., 2001) may lead to a rapid onset of anaerobic methanogenesis.

Seasonal patterns of CH₄ uptake at our study site were weak, similar to those in many other forests (Tang et al., 2006; Morishita et al., 2007; Liu et al., 2008; Zhang et al., 2008). Seasonal CH₄ uptake by soils was correlated with SWC (Fig. 2b), especially during the dry season (Fig. 3d). This result is consistent with results found in slash pine plantations in Florida (Castro et al., 2000) and many other forest types (Castro et al., 1994a; Steinkamp et al., 2001; Butterbach-Bahl et al., 2004; Curry, 2007; Liu et al., 2008; Yan et al., 2008; Zhang et al., 2008; Guckland et al., 2009; Rowlings et al., 2012). The primary reason is that SWC affects soil gas diffusivity (Marrero and Mason, 1972), which is considered the primary factor in regulating atmospheric CH₄ uptake by soils (Striegl, 1993; Brumme and Borken, 1999). Furthermore, low SWC, not extreme drought, has a limited effect on CH₄ uptake by forest soils (Saari et al., 1998). In addition, we found that high SWC could turn soil into a CH₄ source (Fig. 1a) as similar as other forests (Yan et al., 2008). Contrary to our results, a relationship between CH₄ uptake and SWC was not found in tropical montane forests, possibly because of the absence of a pronounced dry season and small variations in SWC across the whole year (Wolf et al., 2011).

T_S had no effect on CH₄ uptake in our study (Fig. 1) though microbial activity in soils depends on temperature (Conrad, 1996). Our result was supported by several previous studies (Born et al., 1990; Priemé and Christensen, 1997; Borken et al., 2000; Smith et al., 2000; Tang et al., 2006; Morishita et al., 2007; Peichl et al., 2010). The no dependencies of CH₄ uptake on T_S may be attributed to substrate (atmospheric CH₄) limitation that is controlled by gas diffusivity in soils and low atmospheric CH₄ concentration, as indicated by Smith et al. (2000).

In our study, annual atmospheric CH₄ uptake by the soil was about 125 mg CH₄ m^{-2} year^{-1}. The CH₄ uptake strength here was comparable to that reported for tropical forest soils in China (Zhang et al., 2008), German forests (Borken and Brumme, 1997; Smith et al., 2000), temperate and subtropical forest soils in Japan (Morishita et al., 2007) and boreal forests in Siberia (Flessa et al., 2008). However, the strength of CH₄ uptake at our study site was
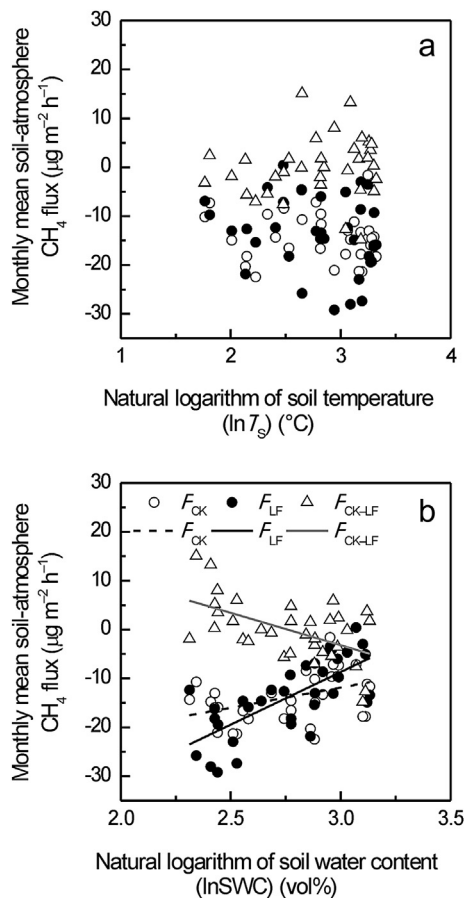

Fig. 2. Responses of monthly mean soil-atmosphere CH₄ fluxes (F_{CK}, F_{LF} and F_{CK-LF}) to natural logarithms of (a) soil temperature ($P = 0.21–0.40$) and (b) water content. In subfigure (b), the three relationships are: $F_{CK} = 8.3 * \ln SWC - 36.6$, $R^2 = 0.17$, $P = 0.015$; $F_{LF} = 21.5 * \ln SWC - 73.3$, $R^2 = 0.51$, $P < 0.001$; and $F_{CK-LF} = -13.3 * \ln SWC + 36.7$, $R^2 = 0.29$, $P < 0.001$. When SWC = 15.8 vol%, $F_{CK-LF} = 0$.
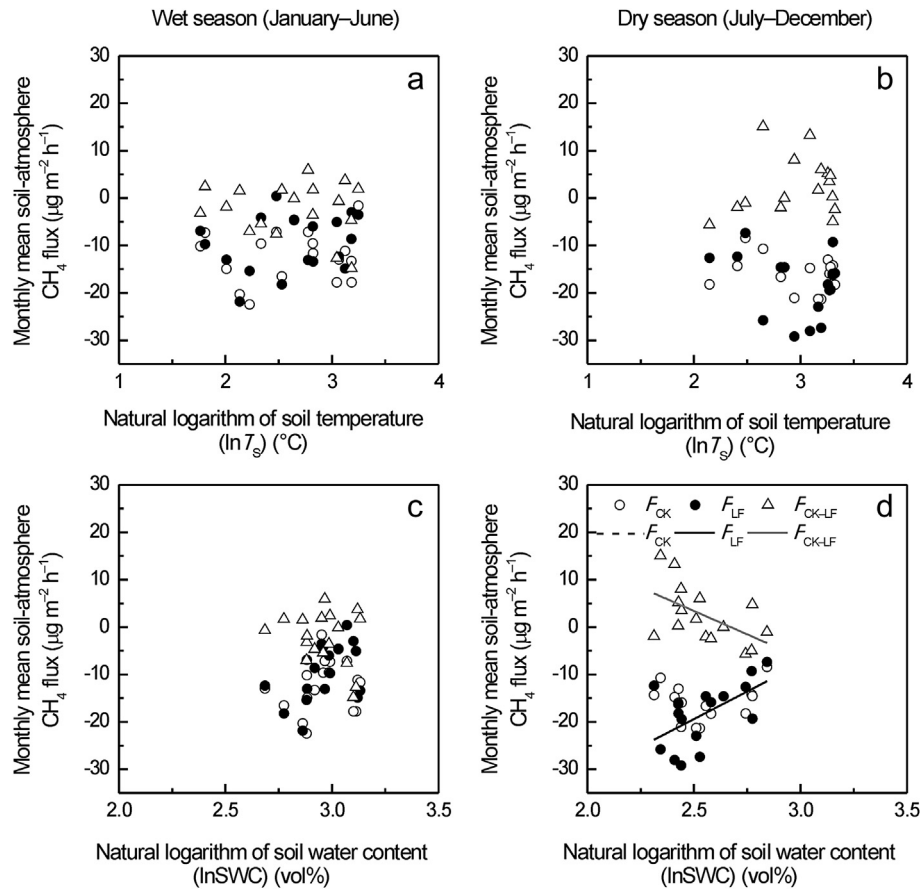
Fig. 3. Dependence of monthly mean soil-atmosphere CH_4 fluxes (F_{CK}, F_{LF} and F_{CK-LF}) on (a and b) soil temperature ($P = 0.24–0.66$) and (c and d) water content during the wet and dry seasons, respectively. In subfigure (d), the two relationships are: $F_{LF} = 23.3*lnSWC - 77.6$, $R^2 = 0.32$, $P = 0.02$; $F_{CK-LF} = -19.8*lnSWC + 52.8$, $R^2 = 0.29$, $P = 0.03$.

also much lower than values found in other forest ecosystems (Adamsen and King, 1993; Castro et al., 1994b; Saari et al., 1998; Price et al., 2003; Tamai et al., 2003; Tang et al., 2006; Liu et al., 2008; Guckland et al., 2009; Wolf et al., 2011). The differences found among these studies could be due to differences in age (Peichl et al., 2010; Hiltbrunner et al., 2012), coniferous characteristics (Degelmann et al., 2009), or past disturbance reforestation (Price et al., 2003).

4.2. Effect of litter layer on CH₄ uptake

The litter horizon acts as single diffusion barriers, lowering atmospheric CH_4 uptake by soils (1.3–2.7-fold), in a boreal pine forest (Saari et al., 1998) and in temperate forests (Borken and Brumme, 1997; Dong et al., 1998; Brumme and Borken, 1999; Steinkamp et al., 2001; Price et al., 2003), especially during dry soil conditions (Peichl et al., 2010). In this study, we also found evidence that litter can act as a barrier when SWC was below the threshold (15.8 vol%), likely because this horizon impede gas exchange between the soil and the atmosphere (Brumme and Borken, 1999). Contrary to these previous studies, however, we found that the litter layer can also increase atmospheric CH_4 uptake by soil when SWC was above a certain threshold (15.8 vol%). This idea is supported by work by Borken and Beese (2006), who suggested that litter may benefit the gas diffusivity of the mineral soil by storing some rainfall. Rainfall frequency at our study site is 75–100 days year^{-1} (Wang et al., 2012b). About 70% of precipitation occurred in the wet season (Wang et al., 2012a). During the wet seasons, it appears that the litter layer holds rainfall and benefits gas diffusivity of the

mineral soil at our study site. Furthermore, under wet soil conditions, high SWC suppressed CH_4 uptake by mineral soil (Fig. 2b); while litter layer may have a relatively higher contribution total CH_4 oxidation by forest soils such as tropical montane forest soils (Wolf et al., 2011).

At the annual scale, we found that the litter layer had a minimal effect on CH_4 uptake by soils. This result was supported by several studies in southern China also using litter removal methods (Tang et al., 2006; Liu et al., 2008). The main interpretation by these authors was that microbial CH_4 oxidation was mainly related to the mineral soil rather than the litter layer (Saari et al., 1998; Brumme and Borken, 1999; Steinkamp et al., 2001). In contrast, we found that the litter layer acted as a moisture-induced bidirectional buffer for CH_4 consumption by the soils. Canceling effects during the wet and dry seasons generate a minimal annual effect. The balance of these effects is likely to change in the future due to climate change.

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