Science of the Total Environment 849 (2022) 157891

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Litter-derived nitrogen reduces methane uptake in tropical rainforest soils

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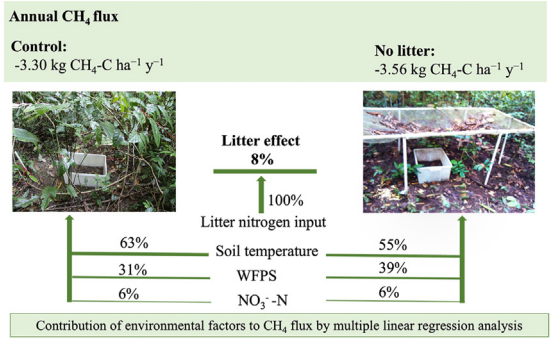
HIGHLIGHTS

- Existence of litter layer decreased soil CH_4 uptake by 8 % in tropical rainforest, SW China.
- Litter removal effect on soil CH_4 uptake was mainly regulated by LNI 100 %.
- Soil inorganic nitrogen content explained 84 % of litter effect on soil CH_4 uptake in forest ecosystems.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Zhaozhong Feng

Keywords:
Methane
Inorganic nitrogen content
Litter decomposition
Litter removal
Tropical rainforest

ABSTRACT

Litter comprises a major nutrient source when decomposed via soil microbes and functions as subtract that limits gas exchange between soil and atmosphere, thereby restricting methane (CH4) uptake in soils. However, the impact and inherent mechanism of litter and its decomposition on CH4 uptake in soils remains unknown in forest. Therefore, to declare the mechanisms of litter input and decomposition effect on the soil CH4 flux in forest, this study performed a litter-removal experiment in a tropical rainforest, and investigated the effects of litter input and decomposition on the CH4 flux among forest ecosystems through a literature review. Cumulative annual CH4 flux was −3.30 kg CH4-C ha^{-1} y^{-1}. The litter layer decreased annual accumulated CH4 uptake by 8% which greater in the rainy season than the dry season in the tropical rainforest. Litter decomposition and the input of carbon and nitrogen in litter

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http://dx.doi.org/10.1016/j.scitotenv.2022.157891
Received 9 May 2022; Received in revised form 13 July 2022; Accepted 4 August 2022
Available online 8 August 2022

biomass reduced CH4 uptake significantly and the difference in CH4 flux between treatment with litter and without litter was negatively associated with N derived from litter input. Based on the literature review about litter effect on soil CH4 around world forests, the effect of litter dynamics on CH4 uptake was regulated by litter-derived nitrogen input and the amount soil inorganic nitrogen content. Our results suggest that nitrogen input via litter decomposition, which increased with temperature, caused a decline in CH4 uptake by forest soils, which could weaken the contribution of the forest in mitigating global warming.

1. Introduction

Methane (CH_4), a major greenhouse gas in the atmosphere, is mainly produced by the anaerobic decomposition of organic matter in soil (Lelieveld et al., 1993). Although soil is the largest active CH_4 sink in forest ecosystems, any given soil can be either a source or sink for atmospheric CH_4; this is determined by the relative production of CH_4 by methanogens and the oxidation of CH_4 by methanotrophs, processes that occur simultaneously in soils where aerobic and anaerobic microsites coexist (Yavitt et al., 1993; Topp and Pettey, 1997; Dutaur and Verchot, 2007; Wolf et al., 2012). The global annual CH_4 flux is 21(18–26) as emissions and global soil uptake of CH_4 is 37(range: 27–43) and 30 (range:11–49) from bottom-up and top-down estimations approaches, respectively (in Tg CH_4 yr^{-1}) (Canadell et al., 2021). The annual global uptake of CH_4 in forest soils from 1981 to 2010 has been estimated to be 9.16 ± 3.84 Tg CH_4 yr^{-1} (Yu et al., 2017). Therefore, it is believed that forest soils provide a significant sink for methane and help mitigate climatic warming.

The observed CH_4 fluxes in forest ecosystems are mainly net balance between methanogenesis and methantrophic activities. Hence, various factors such as temperature, soil water content, soil texture, pH, soil inorganic nitrogen (N) content, microbial activity and fertility etc.(Schnell and King, 1994; Castro et al., 1995; Tamai et al., 2003; Zhang et al., 2008; Giri et al., 2014; Leitner et al., 2016; Martins et al., 2017) could affect these two processes via different mechanisms and further affect on the CH_4 flux. Litter provides numerous exogenous nutrients to soil microbes during its decomposition (Dong et al., 1998; Wang et al., 2013) and leaching (Zhou et al., 2016). The decomposition of litter, followed by the incorporation of the resulting organic matter into the soil, provides the energy requirements of methanogens (Zheng et al., 2017) in forest ecosystem without fertilizer. Therefore, litter input will greatly influence soil CH_4 flux in forest ecosystems. For example, litter removal significantly increased CH_4 uptake rates in soils of temperate forests in Germany (Dong et al., 1998) and Austria (Leitner et al., 2016) and in soils of a beech forest and a deciduous forest in Canada, and a pine forest in Finland (Peichl et al., 2010), and Finland (Saari et al., 1998) in pine forest, whereas litter input in a subtropical forest in China had no effect on CH_4 flux (Tang et al., 2006). Conversely, litter removal from the forest floor reduced CH_4 uptake in four soils under pure beech and two mixed forests (30 % spruce, 70 % beech and 70 % spruce, 30 % beech) in Germany (Borken and Beese, 2006). Thus, the potentially important impact of litter on CH_4 flux in soils varied among forest types. Although the differential responses of CH_4 flux in response to litter removal may be associated with the variations in the physiochemical properties of the studied forest soils and litter layers, litter dynamics (litter production and decomposition) and the effects of environmental factors on litter decomposition (Gritsch et al., 2016), the mechanisms of litter input effect on CH_4 flux remain to be elucidated. Therefore, further research is wanted to study the effects of litter layer on CH_4 uptake in the soils of forested ecosystems.

Previous studies have examined litter contribution to soil CH_4 flux (Dong et al., 1998; Saari et al., 1998; Borken and Beese, 2006; Tang et al., 2006; Peichl et al., 2010; Leitner et al., 2016) and variations in soil temperature, soil water content (Yan et al., 2008; Werner et al., 2006), soil inorganic N content, and soil microbial activities affect CH_4 flux in forest soils among forests ecosystems. However, only few field experiments have evaluated the influence of litter dynamics on soil CH_4 flux in forest, particularly the possible effects of nitrogen and carbon derived from litter decomposition on CH_4 flux versus the role that soil fertility or environmental factors plays (Corteselli et al., 2017). Therefore, further research on the effects of litter decomposition and nutrient input on CH_4 uptake in forest soils is urgently required to better understand the mechanisms underlying the exchange of CH_4 at the soil–atmosphere interface among forest.

Tropical forests are generally considered to be a major net sink for CH_4 (Tian et al., 2016; Tian et al., 2019; Tian et al., 2020). The annual CH_4 uptake by tropical forests is estimated to be 6.4 Tg yr^{-1}, which accounts for 45 % of global CH_4 uptake by forest soils (Dutaur and Verchot, 2007). Furthermore, the production and oxidation of CH_4 in tropical forests are more sensitive to the carbon and nitrogen input because of the higher rainfall and temperature. The reason is that soil available carbon and CO_2 are the main substrates for CH_4 production and nitrogen content also influence the soil microbial function which introduces more carbon inputs into the soil during rainy season via throughfall deposition (Yu et al., 2021; Zhou et al., 2016). Therefore, nitrogen content is correlated to CH_4 production and oxidation; and has a strong relationship with CH_4 flux. Tropical rainforests produce much more litter and decompose it more rapidly than temperate and boreal forests (Tang et al., 2010). For tropical rainforest without fertilizer, litter is the main source for soil carbon and nitrogen. However, few studies regarding the litter input effect on soil CH_4 fluxes have focused on tropical rain forests (Yan et al., 2008; Lang et al. 2017; Yu et al., 2021; Zhou et al., 2021). In addtion, the accuracy of CH_4 flux modelling in tropical regions is affected, to some extent, by our poor understanding of the contributions of litter input and decomposition to the soil CH_4 flux (Tian et al., 2016). Therefore, the mechanisms of litter input and decomposition effect on the soil CH_4 flux in tropical forests need to be better understood. In this study, we (1) performed a litter-removal experiment that measured litter dynamics (litter production and decomposition) and soil physicochemical properties in a tropical rainforest, southwest China, and (2) investigated the effects of litter input and decomposition on the CH_4 flux among forest ecosystems through a literature review.

2. Materials and methods

2.1. Study site

The tropical rainforest we studied is belonged to CNERN (Chinese National Ecosystem Research Network) and CERN (ChinaFLUX) located in Xishuangbanna, Yunnan Province, southwest China (21°10′ N, 101°2′ E, elevation 650 m). Mean annual precipitation for the study period (2003–2016) was 1415 mm and mean annual air temperature was 21.4 °C (Fei et al., 2018). The climate of this area is tropical monsoon, characterised by a strong seasonal variation in precipitation, with >80 % of precipitation falling in a distinct rainy season (May–October). During the study period, the mean air temperature was 19.9 °C (a bit below normal), and the mean precipitation was approximately normal (1412 mm). The soils of the study area are mainly comprised of oxisols derived from Cretaceous yellow sandstone. Surface soil (0–20 cm) bulk density was 1.4 ± 0.1 g cm^{-3}. Soil texture was sandy loam with 60 % of sand, 17 % of silt, and 23 % of clay. The pH was 4.6. The total N and organic contents were 1.1 ± 0.1 and 9.2 ± 2.2 g kg^{-1}, respectively. The dominant tree species are *Terminalia myriocarpa*, *Barringtonia pendula*, *Pometia tomentosa*, *Amoora tetrapetala*, *Gironniera subaequalis* and *Mitrephora maingayi* (Cao et al., 1996).

2.2. Experimental design

We performed a litter-removal experiment to investigate the influence of litter input on CH_4 flux in tropical rainforest soil. The study sites were

divided into treatment areas where litter was removed (NL) (i.e., not allowed to accumulate) and control sites (L) where litter accumulated naturally. A paired-plot design was used where a pair of L and NL plots was selected within an area of 20 m × 20 m. Locations of six paired plots (i.e., six replicates) were randomly selected and a distance of >100 m was kept between the pairs. In the litter-removal treatments, the litter layer was carefully removed (i.e., no disturbance in the mineral soil profile) from the soil surface 3 months prior to initiating measurements. To prevent newly produced litter from accumulating, we installed nylon nets (2.0 mm mesh, 1 × 2 m in dimension) 1.5 m above each plot. Litter collected in these nylon nets were removed weekly prior to CH_4 flux measurements.

2.3. Soil CH_4 flux measurements

Soil CH_4 fluxes were simultaneously measured at weekly intervals for L and NL treatments using static opaque chambers. One permanent polyvinyl chloride (PVC) base collar (0.3 × 0.4 m) was placed in the centre of each field plot (six collars in L plots and six in NL plots) and inserted into the soil to a depth of 0.1 m (Tang et al., 2006; Brümmer et al., 2009; Dou et al., 2016). PVC gas chambers, each with an area of 0.12 m^2 and 0.2 m height, were manually secured onto the base collars when measuring gas flux. To measure gas emissions, about 100 ml of gas was manually collected from each chamber with air-tight syringes at 0, 15, 30, 45 and 60 min after the chamber was tightly secured onto the base collars. The sampling campaigns were carried out between 09:00 and 11:00 local time. Within 24 h after gases were extracted, the CH_4 concentration in the gas samples were measured with an Agilent 4890D gas chromatograph (Agilent Technologies, Palo Alto, California, USA) equipped with a flame ionisation detector (FID) (refer to Zheng et al. (2008) for details). The following equation, described by Zhou et al. (2016) was used to calculate the CH_4 flux (negative values indicate uptake):

$$F = \rho \frac{V}{A} \frac{P}{P_0} \frac{T_0}{T} \frac{dC_t}{dt} \quad (1)$$

where F is the CH_4 flux (μg m^{-2} h^{-1}), ρ is the CH_4 density under the ambient air temperature (μg m^{-3}), V is the volume of the chamber (m^3), A is the area of the ground covered by the chamber (m^2), T is air temperature (°C) at the time of sampling, P is atmospheric pressure (hPa) at the time of sampling, T_0 and P_0 were the air temperature and atmospheric pressure under standard conditions (T_0 = 25 °C, P_0 = 1013 hPa), respectively, and C_t is the CH_4 concentration (ppm) in the chamber at time t.

The annual and monthly accumulated CH_4 fluxes (negative values indicate uptake) were calculated as follows (Cai et al., 2013):

$$AF = \Sigma_{i=1}^{n}(F_i + F_{i+1})/2 \times (t_{i+1} - t_i) \times 24 \times 10^{-5} \quad (2)$$

where AF is the annual and monthly accumulated CH_4 flux (kg C ha^{-1}), F is the CH_4 flux (μg m^{-2} h^{-1}), i is the ith measurement, $t_{i+1} - t$ is the number of days between two consecutive measurements and n is the total number of measurements.

Litter effect (LE) on CH_4 uptake was calculated using the following equation:

$$LE = F_L - F_{NL} \quad (3)$$

where F_L and F_{NL} are the CH_4 fluxes from the L and NL treatments, respectively.

Inhibitory effect (IE) of litter layer on the CH_4 uptake was calculated using the following equation:

$$IE = \frac{F_{NL} - F_L}{F_L} \times 100\% \quad (4)$$

2.4. Litter dynamics

2.4.1. Litter production and litter stock

Forty circular, nylon litter traps (1.0 mm mesh size, diameter: 0.8 m, area: 0.25 m^2) were placed randomly on the forest floor to measure litter production in the rainforest. Litter in the traps was collected monthly on the same day that gas flux was measured.

Ten square PVC frames (0.584 m^2 each) were placed randomly on the forest floor, in the vicinity (within 20 m) of the experimental plots, to collect litter stock (LS) on the forest floor. The litter that accumulated in the PVC frames were carefully collected by hands in March, June, September and December from 2013 to 2014. The locations of these frames were changed after each litter sampling event (i.e., March, June, and September).

2.4.2. Litter decomposition

We used the least squares method to calculate monthly litter decomposition rates from the data of litter production and litter mass remaining on the forest floor that was obtained quarterly from LS plots, assuming that the litter decomposition rates were constant between two sampling occasions. Litter biomass input (LBI) was calculated with the information from LP and LS as follows (Gao et al., 2018):

$$LBI_i = (LP_i + LS_{i-1}) - LS_i \quad (5)$$

where LBI is the interpolated monthly litter-derived biomass input (decomposed), LP is litter production in the i month, LS is the litter stock and i is month of the year.

2.5. Carbon and nitrogen input from litter

After oven-drying the collected litter at 40 °C, they were ground by passing it through a 0.25 mm sieve. The carbon (C) and nitrogen (N) content of the ground litter was measured with a Vario MAX CN elemental autoanalyser (Elementary Analysensysteme, GmbH, Langenselbold, Germany). The monthly litter-derived C and N inputs to forest soil were calculated as follows:

$$LNI = LBI_i \times C_{Ni} \quad (6)$$

$$LCI = LBI_i \times C_{Ci} \quad (7)$$

where LNI and LCI are the C and N input from litter (kg ha^{-1} $month^{-1}$), respectively and C_{Ni} and C_{Ci} are the N and C contents (g kg^{-1}) of the litter for month i, respectively.

2.6. Soil sampling and physicochemical analyses

During our sampling of gas emissions, we measured soil (at 0 – 10 cm depth) and air temperatures using a needle thermometer. Soil water content (at 0 – 5 cm depth, V/V%) was detected using a TDR100 time-domain reflectometer (Campbell Scientific, Logan, Utah, USA). Water-filled pore space (WFPS) was calculated as follows:

$$WFPS = SWC/(1 - BD/2.65) \quad (8)$$

where SWC is soil water content (v/v%) and BD is soil bulk density (g cm^{-3}).

Precipitation above the canopy was recorded at 30 min intervals using an automatic recorder fixed on top of an eddy flux tower that was 200 m from our sampled plots.

Soil samples (0–20 cm depth) were collected monthly from L and NL treatments throughout the experimental period. Collected soil was transported to the laboratory in an icebox and stored at 4 °C prior to chemical analyses. After the soil was passed through a 2-mm sieve (where fine roots, debris and stones were removed), we used the KCl-extraction method (soil:water, 1:10) to detect soil NO_3^--N and NH_4^+-N content. We measured microbial carbon (MBC) and dissolved organic carbon (DOC) in the

sampled soil using the chloroform fumigation and K_2SO_4 extraction (0.05 mol $L^{-1}K_2SO_4$) method (soil to water ratio: 1:5) (Jenkinson and Powlson, 1976). More details on the methods for soil physicochemical analyses can be found in Gao et al. (2018).

2.7. Data source for the inhibitory effect comparison

Methane flux data were extracted from published studies that included experiments with litter/organic layer removal treatments (Table S1). We limited the data extraction in field measurement using static chamber method with at least a single year of observations. Ancillary data of NH_4^+-N and NO_3^--N were extracted from figures and tables in the selected studies. If the extracted data had a variation range (spatial and temporal), the mean values of the data were used. The inorganic N content refers to the sum of NH_4^+-N and NO_3^--N. In total, by the literature review, we collected mean annual temperature, mean annual precipitation, bulk density, pH, NH_4^+-N, NO_3^--N, and the CH_4 flux data in litter removal treatment and control from seven studies in a total of nine forests. Regression analyses were performed between the inhibitory effect and the soil inorganic N content (Table S2).

2.8. Statistical analyses

We tested the normality of all data with the Kolmogorov–Smirnov test, followed by linear mixed effects models to assess the treatment effect on monthly CH_4 flux and soil physicochemical properties (soil temperature, WFPS, NO_3^--N, NH_4^+-N, DOC and MBC). The plot number and month were included as random effects to account for the experimental design and the repeated measures, respectively. Relationships between monthly CH_4 flux and measured soil physicochemical properties were explored further with Pearson correlations. We applied a multiple linear regression analysis to explain the relationship between monthly CH_4 flux (dependent variable) and measured soil properties (independent variables). We calculated the R^2 contributions to the covariates using total R^2 and the R^2 of each independent variable. The data are presented as the mean ± 1 SE (standard error). All analyses were performed with SAS® 9.1 for Windows® (SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Litter effect on soil CH_4 flux in tropical rainforest

CH_4 flux from the L and NL treatments showed similar temporal variations, with a higher mean rate of CH_4 uptake occurring in the dry season ($F_L = -47.66 \pm 3.11$ μg CH_4-C m^{-2} h^{-1}, $F_{NL} = -49.11 \pm 2.80$ μg CH_4-C m^{-2} h^{-1}) than during the rainy season ($F_L = -24.87 \pm 2.28$ μg CH_4-C m^{-2} h^{-1}, $F_{NL} = -29.61 \pm 2.16$ μg CH_4-C m^{-2} h^{-1}) (Fig. 1a). The difference in CH_4 flux between L and NL treatments ($F_{L\text{-}NL}$) in soil was significant in the rainy season ($F = 20.353$, $p < 0.001$), and was insignificant in the dry season ($F = 0.922$, $P = 0.339$, Fig. 1b). Cumulative annual CH_4 flux was −3.30 kg CH_4-C ha^{-1} y^{-1} in plots with litter and −3.56 kg CH_4-C ha^{-1} y^{-1} in plots without litter. Thus, without litter accumulation, soils increased their CH_4 uptake by around 8 % annually. According to the monthly total CH_4 flux, the cumulative uptake in the dry season accounted for 64 % and 61 % of the annual CH_4 uptake in plots with litter (L) and those without litter (NL), respectively (Fig. 2a). The effect of an absence of litter on soil CH_4 uptake was greater in the rainy season than in the dry season (Fig. 2b).

3.2. Factors influencing of soil CH_4 flux in tropical rainforest

Soil CH_4 flux was significantly and positively correlated with soil temperature, WFPS, rainfall and soil NO_3^--N content in both treatments (with and without litter) (Table 1). Litter biomass, carbon and nitrogen input were positively associated with the CH_4 flux (Table 1), suggesting that litter decomposition and the input of carbon and nitrogen in litter

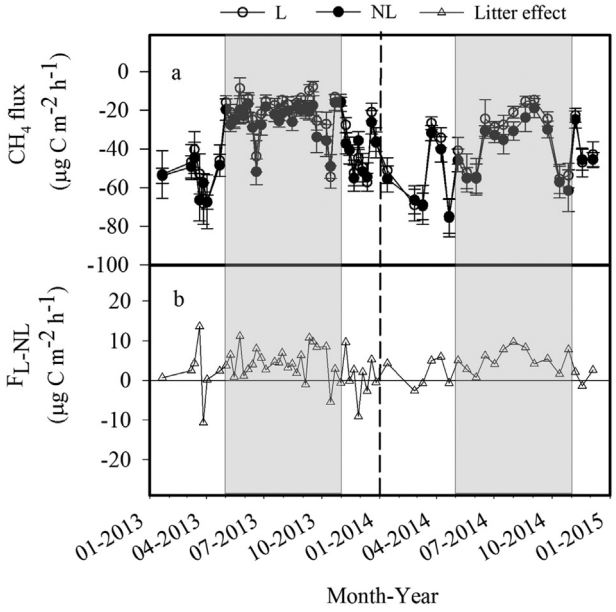

Fig. 1. Soil CH_4 flux in treatments with litter (L) and with litter removal (NL) treatment (a) and the litter effect on soil CH_4 flux ($F_{L\text{-}NL}$) (b). Sign convention, negative means uptake of CH_4 from the atmosphere.

biomass reduced CH_4 uptake in plots where litter accumulated. Multiple linear regressions showed that soil CH_4 fluxes in both L and NL treatments were negatively associated with a combination of soil temperature, soil moisture, soil N fraction, soil C fraction and C and N inputs from litter biomass. However, $F_{L\text{-}NL}$ was negatively associated with N derived from litter input (LNI) (Table 2).

3.3. The inhibitory effect of litter on soil CH_4 uptake

The inhibitory effect of litter layer on soil CH_4 uptake ranged from −3 % to 49 % in forest ecosystems worldwide. According to the Pearson correlation, the inhibitory effect of litter layer on soil CH_4 uptake was significantly and negatively associated with mean annual temperature ($r = -0.805$, $p = 0.009$), soil NH_4^+-N ($r = -0.686$, $p = 0.041$) and soil inorganic nitrogen ($r = -0.700$, $p = 0.036$) based on data from studies around the world (Table S1). The soil inorganic N content explained the inhibitory effect of litter on soil CH_4 uptake (84 %) with an exponential regression

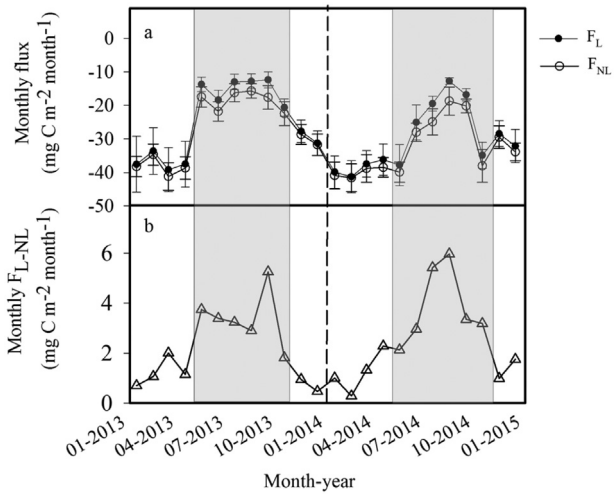

Fig. 2. Monthly accumulated CH_4 flux in plots with (F_L) and without (F_{NL}) litter (a) the difference of CH_4 flux between L and NL (F_L-F_{NL}) and (b) in forests soils.

Table 1
Pearson correlation coefficients between environmental variables and monthly CH_4 flux in a tropical rainforest in southwest China.

	F_L	F_{NL}
T_{soil}	0.76**	0.71**
WFPS	0.81**	0.84**
Rainfall	0.76**	0.75**
NH_4^+-N		
NO_3^--N	0.55**	0.56**
DOC		
MBC		
LBI	0.57**	
LCI	0.57**	
LNI	0.59**	

Abbreviations: F_L and F_{NL} are the CH_4 fluxes from the L (with litter) and NL treatments (without litter), respectively. T_{soil} is soil temperature; WFPS is Water-filled pore space (%); DOC is soil dissolved carbon content; MBC is soil microbial carbon content, LBI is litter-derived biomass input, LCI is litter-derived carbon input, and LNI is litter-derived nitrogen input.
** Correlations that are significant at $P < 0.01$ level of significance.

(Fig. 3). The relationship was better than those between the inhibitory effect and annual temperature ($IE = 54.42 \times \exp^{(-0.13 \times MAT)}$, $R^2 = 0.57$) as well as between the inhibitory effect and NH_4^+-N ($IE = 41.35 \times \exp.^{(-0.406 \times N}H^{4+)}$, $R^2 = 0.73$) .

4. Discussion

4.1. Soil CH_4 uptake in southwest China tropical rainforest soils

Over the 2-year study period, measurements of CH_4 flux from soils with and without litter revealed the rainforest soils are a net sink of atmospheric CH_4. This result is in line with studies conducted in a variety of tropical forests worldwide (Table S2). Prior studies have confirmed that CH_4 flux from soil is mainly regulated by a combined effect of soil water content and soil texture, both of which also influence O_2 concentrations and CH_4 diffusivity between soil and atmosphere (Wolf et al., 2012; Wang et al., 2013), soil inorganic N content (because inorganic N inhibits CH_4 uptake in soils (King and Schnell, 1994; Wang and Ineson, 2003)) and pH (influences microbial activities of methanogens and methanotrophs (Dalal and Allen, 2008). In our study, mean annual precipitation, which is closely related with soil water content (Gao et al., 2018) (Table S3), was the lowest (1412 mm) of all reported values for tropical forests (ranges from 1412 to 5300 mm with a mean of 2669 mm, Table S2). However, soil pH (4.6) and soil inorganic N content (9.13 mg N kg^{-1}) were similar to the means determined for these parameters in tropical forest soils (pH ranges from 3.6 to 6.9 with a mean of 4.7 and inorganic N concentration ranges from 0.85 to 35.1 mg N kg^{-1} with a mean of 14.85 mg N kg^{-1})). The annual CH_4 uptake from the tropical forest soils in our study (-3.3 kg CH_4-C ha^{-1} y^{-1}) was

Table 2
Results of multiple linear regression analysis between monthly soil–atmosphere CH_4 flux and soil variables in tropical rainforest, southwest China.

Model	R^2	*F*	*P*	Covariate	Parameter estimation	R^2 contribution (%)
F_L	0.87	38.46	<0.001	Soil T	1.63	63
				WFPS	0.38	31
				NO_3^--N	1.39	6
F_{NL}	0.85	34.14	<0.001	Soil T	1.25	55
				WFPS	0.38	39
				NO_3^--N	1.02	6
$F_{L\text{-}NL}$	0.44	15.89	<0.001	LNI	1.74	100

Abbreviations: F_L and F_{NL} are the CH_4 fluxes from the L (with litter) and NL treatments (without litter), respectively. $F_{L\text{-}NL}$ is the litter effect on CH_4 fluxes; Soil T is soil temperature; WFPS is Water-filled pore space (%); LNI is litter-derived nitrogen input.

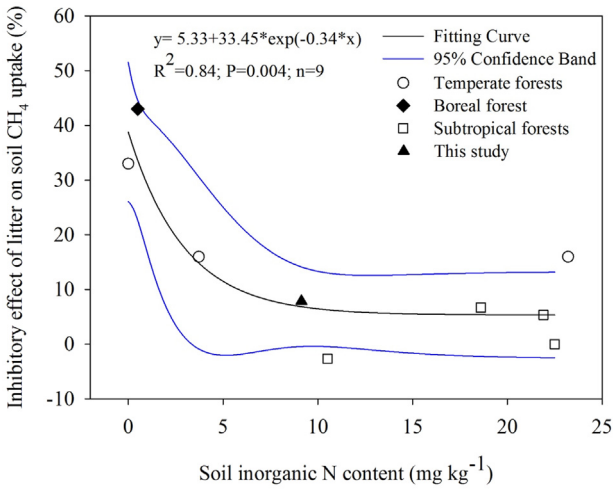

Fig. 3. Relationship between soil inorganic N content and the inhibitory effect of litter on soil CH_4 uptake in various forest ecosystems.

similar to the CH_4 uptake found in a global survey by Dutaur and Verchot (2007) (-3.3 kg CH_4-C ha^{-1} y^{-1}). Our estimate is also within the range of CH_4 flux (-0.5–5.9 kg CH_4-C ha^{-1} y^{-1}) from tropical forests around the world from 1994 to 2016 (Table S2). For forest ecosystems around the world, the differences in CH_4 fluxes between the litter removed treatment and control plots around the world forest ecosystems are due to the combined effects of MAP, inorganic N content and pH, but the most important factor is MAP according to the multiple linear regression ($t = -2.48$, $p = 0.089$) among sites (Table S2). This also suggests that higher annual precipitation may reduce CH_4 uptake in tropical forest soils. Therefore, as a possible effect of global climate change, the increases in precipitation and nitrogen deposition in tropical regions are likely inhibit to CH_4 uptake in tropical forest soils.

Our finding showed that tropical forest soils have higher CH_4 uptake in the dry season than in the rainy season, which is consistent with many other studies in tropical forests (Keller and Reiners, 1994; Steudler et al., 1996; Verchot et al., 2000; Butterbach-Bahl et al., 2004; Keller et al., 2005; Davidson et al., 2008; Kiese et al., 2008; Sousa Neto et al., 2011; Veldkamp et al., 2013; Vanitchung et al., 2014; Jones et al., 2016). Our results suggest that this seasonal pattern is potentially regulated by seasonal variations in water-filled pore space, soil temperature and soil NO_3^--N content (Table S3).

Soil water content is an important factor regulating CH_4 uptake in soil. When soil moisture is high, gas diffusion rates between soil and atmosphere are reduced, and thereby restricts substrate availability (CH_4 from the atmosphere), which then supplies energy for methanotrophs. However, anaerobic microsites in soils with limited O_2 provide ideal conditions for methanogens, which in turn leads to a reduction in the uptake of CH_4 in wet soils during the rainy season under relatively more anaerobic environment (Wolf et al., 2012; Wang et al., 2013). Our finding that CH_4 uptake in soils was negatively associated with soil temperature in plots both with and without litter is consistent with the findings of another study of a tropical montane rainforest in Peru (Jones et al., 2016).

There are two primary reasons why soil temperature is important to CH_4 production rates. First, methanogens are more sensitive to low temperatures than methanotrophs (Segers, 1998) because methanogens are more active at higher temperatures and thus more CH_4 is produced than is consumed at higher soil temperatures. Second, higher soil temperature stimulate respiration by soil microbes, which results in the depletion of soil oxygen concentrations. The depletion of soil O_2 results in an increase in soil anaerobiosis (Butterbach-Bahl et al., 2013), which favours methanogens (and CH_4 production) and inhibits CH_4 consumption, possibly explaining the positive relationship found between CH_4 and CO_2 fluxes in our treatment plots (with and without litter) (Fig. S1).

Our finding that CH_4 uptake is significantly (and negatively) associated with soil NO_3^--N content is consistent with other studies conducted in tropical rainforests such as in Panama (Veldkamp et al., 2013) and Peru (Jones et al., 2016). Two possibilities exist for this negative association: (1) nitrifying bacteria and methanotrophs compete for O_2 (an electron acceptor), thereby leading to an increase in soil NO_3^--N content and a further depletion of soil oxygen, which in turn leads to higher CH_4 production and lower CH_4 consumption (Wang and Ineson, 2003) and (2) methanotrophs are inhibited by the toxic effects of NH_2OH (produced by the oxidation of NH_4^+-N) and NO_2^- (produced by the reduction of NO_3^--N) in tropical forests (King and Schnell, 1994) with higher precipitation.

4.2. Effect of litter on CH_4 uptake in tropical soils

Plots without litter layers had higher annual CH_4 uptake than plots with litter and the result was similar to those from a mixed pine/hardwood forest and a broadleaf forest in southern China (Tang et al., 2006). However, difference in CH_4 uptake rate between L and NL treatments in this study is greater than the differences found in subtropical pine forests in China (Liu et al., 2008; Wang et al., 2013), but less than that found in temperate and boreal forests (Dong et al., 1998; Peichl et al., 2010; Leitner et al., 2016). The difference is also much lower than that found in a temperate beech forest in New Zealand (Price et al., 2004) and a temperate pine forest in Finland (Saari et al., 1998) (Table S1). However, the inhibitory effect of the litter layer on CH_4 uptake in the Boreal forests of Finland (Saari et al., 1998) (49 %) was higher than those found in the temperate forests of Canada (Peichl et al., 2010) (16 %), although soils in those forests were similar in terms of pH, bulk density and litter mass. While the litter mass may not reasonably explain differences in CH_4 uptake among forest ecosystems; this was also suggested by Wolf et al. (2012) after examining CH_4 uptake in three types of tropical rainforests in southern Ecuador. This insight suggests that other environmental factors are responsible for how a litter layer impacts CH_4 uptake in forest soils. As discussed above, the mean annual temperature, mean annual precipitation, NH_4^+-N, NO_3^-—N, pH and inorganic nitrogen (NH_4^+ and NO_3^-) may regulate influence on CH_4 uptake. But according to the literature review and analysis (Table S2, Fig. 3), soil inorganic N content explained a higher proportion (84 %) of variances associated with the effects of litter on CH_4 uptake in various forest ecosystems (Fig. 3) than mean annual temperature and soil NH_4^+-N content. This is also supported by an in situ N addition experiment experiment at the same site (Zhou et al., 2021), which showed N addition significantly decreased soil CH_4 uptake (N addition: -0.0407 ± 0.01543 μg C m^{-2} h^{-1}; Control: -0.0500 ± 0.02083 μg C m^{-2} h^{-1}; $F = 11.327$, $p < 0.001$) when soil nitrogen fractions increased significantly (Zhou et al., unpublished, Fig. S2). Considering that the soil CH_4 flux was significantly correlated to soil mineral N content ($F\ CH_4 = -109.246 + 11.578 \times$ Mineral N ($F = 4.390$, $p = 0.043$)), we concluded that variations in CH_4 uptake among different forest ecosystems are largely due to soil inorganic N content rather than the differences in mean annual temperature and NH_4^+—N. However, among the sites included in our analysis, only one of them is a tropical forest (this study). Therefore, more work should be done to test the inherent mechanism between CH_4 uptake and inorganic N dynamics caused by litter input in unfertilized forest soils, especially in soils of tropical forests.

4.3. Factors influencing the effect of litter on CH_4 uptake

We found that the effect of litter input on CH_4 uptake in forest soils were greater in the rainy season than in the dry season (Fig. 2b). This may be attributed to that 1) soil CH_4 uptake generally occurs in the mineral soil rather than in the overlying litter layer (Saari et al., 1998; Brumme and Borken, 1999; Wang et al., 2013), and 2) the temporal differences of environmental factors (Gao et al., 2018) that control CH_4 uptake between L and NL should respond to seasonal variations of litter effect on soil CH_4 uptake (Table 1). The reasons are as following. Firstly, litter removal only suppresses net CH_4 flux in soils and does not change the mechanism governing the flux (Figure1, Table 1) as litter removal from experimental plots did not change any relationship between soil properties and the CH_4 flux. Secondly, water-filled pore space, soil temperature, MBC and N fractions varied slightly over time in plots both with and without litter (Gao et al., 2018). In this way, temporal fluctuations in the effect of litter on CH_4 uptake is controlled by the amount of litter input at any given time and the process of decomposition (Tables 1, 2). Furthermore, multiple regression analysis revealed that N input from litter was the dominant environmental factor influencing the effect of litter on CH_4 uptake (Table 2), indicating that the temporal variation in litter-derived nitrogen input to soils is responsible for the temporal variation in the CH_4 flux. Although 51 % of the annual total litterfall was produced in the dry season at our study site, higher precipitation and temperatures in the rainy season were responsible for 68 % of litter decomposition that occurred (Gao et al., 2018). Dissolved inorganic nitrogen and dissolved organic nitrogen flux (Fig. S3) were also higher during the rainy season. Prior research conducted in the same forest reported significantly positive correlations between dissolved nitrogen content and the rate of litter decomposition (Zhou et al., 2015), indicating that more labile nitrogen (derived from litter decomposition) is input to the soil during the rainy season than in the dry season. Since the annual throughfall of dissolved inorganic nitrogen (from September 2013 to August 2014) was 6.78 kg ha^{-1} yr^{-1} (Yu et al., 2021) which was far less than litter decomposition input (139.80 kg ha^{-1} $year^{-1}$) at the site (Gao et al., 2018), we suggest that the inorganic N from litter decomposition was the major inhibitor of soil CH_4 uptake. The results also suggest that if increases in temperature and rainfall occur as a result of climate change, the subsequent increase in decomposition rates could have a negative impact on CH_4 uptake in forests soils and weaken the contribution of forests in mitigating global warming.

5. Conclusions

In this study, we evaluated the effect of litter layers and litter decomposition dynamics on CH_4 uptake on tropical rainforest soils. Our results showed that temporal variations in CH_4 uptake were mainly regulated by soil temperature, soil moisture and soil nitrate content. Litter removal did not change the mechanisms responsible for CH_4 flux, but it did increase CH_4 uptake by eliminating exogenous nitrogen inputs to soil that were derived from litter decomposition. Litter had a more significant effect on CH_4 uptake during the wet season that during the dry season, possibly because the higher nitrogen input from litter decomposition occurred during the rainy season. Our study suggests that the variation in CH_4 uptake in response to litter removal in forest ecosystems is likely more regulated by soil inorganic nitrogen content than the properties of litter layers themselves. Altogether, we can deduce that future climate warming is likely to stimulate litter-derived nitrogen input to soil, eventually leading to a reduction in CH_4 uptake by forests.

CRediT authorship contribution statement

Jinbo Gao and Wenjun Zhou conducted the experiments, analysed the data and wrote the manuscript. Yingping Zhang, Junbin Zhao, Yuntong Liu, Liqing Sha, Youxing Lin, Heng Gui, and Qinghai Song helped design the experiment and write the manuscript. Guirui Yu, Junhui Zhang, Xunhua Zheng, Yunting Fang, John Grace, Jianchu Xu, Junbin Zhao and Fergus Singlar assisted the manuscript writing.

Data availability

No data was used for the research described in the article.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors declare no competing interests. All data, generated or analysed during this study, are included in this article and the supporting information. This work was supported by National Natural Science Foundation of China (42073080, 31870467, 31770528, 42165009), the National Natural Science Foundation of China and Thailand Research Fund (NSFC-TRF) (41961144017), the Scientific Research Funding of Yunnan Provincial Department of Education (2020J0645) and Yunnan Provincial Department of Scientific and Technology (202205AC160045) China and Open Funding from CAS Key Laboratory of Tropical Forest Ecology. We also thank the postdoctoral project (2021) of Department of Human Resources and Social Security of Yunnan. We appreciate the staffs and technicians of the Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies and students of the Climate Change Research Group, XTBG, CAS, for helping with field work. We also thank Institutional Center for Shared Technologies and Facilities of XTBG, CAS for helping us with the soil and litter analyses.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.157891.

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